



SMITHSONIAN

MISCELLANEOUS COLLECTIONS

VOL. 131



"EVERY MAN IS A VALUABLE MEMBER OF SOCIETY WHO, BY HIS OBSERVATIONS, RESEARCHES,
AND EXPERIMENTS, PROCURES KNOWLEDGE FOR MEN"—JAMES SMITHSON

(PUBLICATION 4310)

CITY OF WASHINGTON
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LEONARD CARMICHAEL,
Secretary, Smithsonian Institution.

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6. GAZIN, C. LEWIS. Paleocene mammalian faunas of the Bison Basin in south-central Wyoming. 57 pp., 16 pls., 2 figs. Feb. 28, 1956. (Publ. 4229.)
7. GAZIN, C. LEWIS. The upper Paleocene Mammalia from the Almy formation in western Wyoming. 18 pp., 2 pls. July 31, 1956. (Publ. 4252.)
8. GAZIN, C. LEWIS. The geology and vertebrate paleontology of upper Eocene strata in the northeastern part of the Wind River Basin, Wyoming. Part 2. The mammalian fauna of the Badwater area. 35 pp., 3 pls., 1 fig. Oct. 30, 1956. (Publ. 4257.)
9. KILHAM, LAWRENCE. Breeding and other habits of casqued hornbills (*Bycanistes subcylindricus*). 45 pp., 6 pls., 2 figs. Nov. 8, 1956. (Publ. 4259.)
10. SNODGRASS, R. E. Crustacean metamorphosis. 78 pp., 28 figs. Oct. 17, 1956. (Publ. 4260.)
11. CHADWICK, L. E. The ventral intersegmental thoracic muscles of cockroaches. 30 pp., 18 figs. Jan. 15, 1957. (Publ. 4261.)



SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 131, NUMBER 1

Roebling Fund

LEADING OPERATIONS OF THE
SMITHSONIAN ASTROPHYSICAL
OBSERVATORY, 1895 to 1955

By

C. G. ABBOT

Research Associate, Smithsonian Institution



(PUBLICATION 4222)

CITY OF WASHINGTON
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Koebling Fund

LEADING OPERATIONS OF THE SMITHSONIAN ASTROPHYSICAL OBSERVATORY, 1895 TO 1955

By C. G. ABBOT

Research Associate, Smithsonian Institution

INTRODUCTION

Having been associated with the Astrophysical Observatory almost from its inception in 1890, it seems good to me to print, in small compass in one place, references to the leading researches and instrumental developments carried out there. It may well be that there are now, and will be in future, those who, for one reason or another, may wish to refer to these events, and will appreciate having easy access to the original sources.

The list is far from exhaustive, either as regards the work of the Astrophysical Observatory, or references to it. But I believe it is sufficient to present a fair picture of what has been accomplished.

SECTION A

PART I.—*Improved and new instruments*

- | | |
|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------|
| 1. The bolometer rebuilt and equipped with a balancing device close beside it and at constant temperature. Result: The drift nearly eliminated and the wiggle greatly reduced. | Annals of the Astrophysical Observatory, ¹ vol. 1, pp. 47-56, 105-109, 1900; vol. 3, p. 42, 1913. |
| 2. Galvanometer. Theory investigated and new galvanometer of tenfold sensitiveness built. | Astrophys. Journ., vol. 18, No. 1, July 1903.
Annals, vol. 1, pp. 244-252, 1900. |
| 3. Vacuum bolometer with self-contained Wheatstone bridge built. Result: Several-fold increase of sensitiveness, and increased steadiness. | Annals, vol. 4, pp. 45-64, 1922. |
| 4. Silver-disk pyrheliometer invented. About 100 copies have been | Smithsonian Misc. Coll., vol. 56, No. 19, 1911. |

¹ Hereafter referred to simply as "Annals."

- built, standardized, and sold at cost to observers throughout the world. Repaired at cost and restandardized free when damaged.
5. Water-flow and water-stir standard pyrheliometers invented and used. The world's scale of solar radiation measurements rests on them.² Annals, vol. 3, pp. 47-52, 1913; vol. 7, p. 105, 1954.
Smithsonian Misc. Coll., vol. 95, No. 23, 1937; vol. 111, No. 14, 1949.
 6. Pyranometer invented. Used daily on short-method solar-constant observations. Used by Moore in North Carolina and Chile. Copies made and sold at cost world-wide. Annals, vol. 3, pp. 52-72, 1913; vol. 7, pp. 99-101, 1954.
Smithsonian Misc. Coll., vol. 87, No. 15, 1932; vol. 110, No. 11, 1948.
 7. Honeycomb pyranometer, or melikeron, invented. Used by Abbot and Aldrich on human body, and by Sverdrup in polar regions. Copies made and sold at cost world-wide. Smithsonian Misc. Coll., vol. 66, No. 7, 1916.
Annals, vol. 4, pp. 65-84, 1922; vol. 7, pp. 15-16, 21, 138, 1954.
 8. Balloon recording pyrheliometer invented and used at high altitudes. Smithsonian Misc. Coll., vol. 72, No. 13, 1922.
 9. Two-mirror coelostat invented. Annals, vol. 4, pp. 41, 300, 1922; vol. 5, pp. 43-45, 1932.
 10. Slide-rule extrapolator invented. Constantly used in long-method solar observing. Smithsonian Misc. Coll., vol. 65, No. 4, 1915.
Annals, vol. 4, pp. 347-365, 1922.
 11. High-power lamp and other devices prepared by F. E. Fowle for researches on deep infrared spectrum. Annals, vol. 2, pp. 22-23, 211, 1908.
 12. Highly sensitive radiometer invented for measuring energy spectra of stars. Annals, vol. 4, pp. 84-86, 1922.
 13. A prism of nearly normal wavelength dispersion invented. Annals, vol. 4, pp. 23-25, 274-287, 1922.
 14. The kampometer invented, a highly sensitive instrument for measuring radiation. Astrophys. Journ., vol. 69, pp. 293-311, 1929.
Smithsonian Misc. Coll., vol. 104, No. 14, 1945.
 15. The periodometer invented, a mechanical instrument for discovering periodic changes in data. Astrophys. Journ., vol. 11, No. 2, pp. 135-139, March 1900.
Smithsonian Misc. Coll., vol. 104, No. 22, 1946; vol. 107, No. 19, 1948.
 16. A multiple rotating-sector dia- Smithsonian Misc. Coll., vol. 89, No. 3, 1933.
Smithsonian Misc. Coll., vol. 87, No. 4, 1932.
- Annals, vol. 5, p. 96, 1932.

² A.P.O. modified form of Ångström pyrheliometer is used in daily observations. See Annals, vol. 6, pp. 50-55, 1942.

phragm combination invented, instantly exchangeable, for bolometer work.

17. A continuously variable rotating sector invented, of accurate ratio, for photometry. No published description.
18. A pair of telephoto cameras invented, electrically connected, for simultaneous exposure on flying objects. The invention comprises a belt-focal-plane shutter, surrounding film spools. Shutter and spools operated by a long spring and clockwork. The observer and assistant separated by a measured base line keep both cameras trained. Observer makes a series of exposures by a trigger, and second camera is simultaneously exposed. One camera on public exhibition in Langley case in the West Hall of the Arts and Industries Building, Smithsonian Institution.
19. Apparatus invented for preventing "personal equation" in observing sudden phenomena. The observer notes the sector where, not the times when, the event occurs. Apparatus on public exhibition in Langley case (see above).
20. Automatic recording radiation instruments invented. Annals, vol. 7, pp. 144-146, 1954.

PART 2.—*Various inventions, mainly for military use in World Wars I and II*

1. Variable-speed power-transmission mechanism, Claim 1, allowed "The combination of a driving element, a driven element, and means for establishing, and maintaining constantly, exactly and positively, a desired speed ratio between said elements, or for continuously varying said ratio." U. S. Patent No. 893416 of July 14, 1908.
2. Variable-speed governor. For a clockwork to be of speed varied at will, without stopping, and continuously, through a several-fold range. Used for a Navy project. U. S. Patent No. 2367254 of January 16, 1945.
3. Self-propelled rotating projectile for smooth-bore guns. Combination with smooth-bore ordnance. U. S. Patent No. 1380172, and U. S. Patent No. 1380171, both of May 31, 1921.

4. Gyroscopic navigation instrument. For measuring differences in longitude and latitude without sun or star observations. General Electric Patent No. 1501886 to C. G. Abbot July 15, 1924.
5. Compass and magnetic-dip indicator. Both this and No. 4 used the principle of neutral flotation in liquid, and electric current therethrough for operating. Germans independently discovered the mathematical principle of No. 4 and built such a machine but it failed. An Englishman from National Laboratory examined patent of No. 4, and said it carried superior features. Work on it stopped with the Armistice, November 1918. General Electric Patent No. 1533683 to C. G. Abbot April 14, 1925.
6. Instrument for navigating airplanes by daylight star observations. Stars can be seen with a small telescope in daylight if the telescope field contains the star image. The instrument could be set to contain the star in its field before observing. Twelve stars and two planets were easily observed by W. H. Hoover in New Mexico. E. D. McAlister observed Altair from airplane at 21,000 feet. Built and tested secretly. Never published.
7. Instrument for automatic mapping of airplane course over ocean, to enable return to course of mother ship. The patent, No. 2367254, above cited, was a part of this device. Built and tested secretly. Never published.
8. Solar distilling apparatus. Patent No. 2141330, December 27, 1938.
9. Solar heater. Patent No. 2247830, July 1, 1941.
10. Solar heat collector. Patent No. 2460482, February 1, 1949.

SECTION B

PART I.—*Researches*

1. Bolometric map of infrared solar spectrum. Annals, vol. 1, pp. 5-204, 1900; vol. 5, p. 54, 1932.
Smithsonian Misc. Coll., vol. 82, No. 1, 1929.
2. Dispersion of rock-salt and fluo-rite. (Six-place decimals in re- Annals, vol. 1, pp. 219-237, 253-262, 1900.

- fractive index called ridiculous by Holland physicists. Identical in fifth place with Paschen work, however.)
3. Structure of water-vapor bands ω_1 and ω_2 . *Annals*, vol. 1, pp. 263-264, 1900.
 4. Total solar eclipses, 1900, 1901, 1908, 1918, 1919. *Astrophysical Observatory special eclipse volume*, 1900.
Annals, vol. 2, p. 2, 1908; vol. 3, pp. 3-6, 1913; vol. 4, pp. 29, 31, 34, 35, 1922.
Smithsonian Misc. Coll., vol. 69, No. 9, 1919.
 5. Theory of sensitive galvanometer. *Annals*, vol. 1, pp. 244-252, 1900.
Astrophys. Journ., vol. 18, No. 1, July 1903.
 6. "The cheapest form of light." *Annals*, vol. 2, p. 5, 1908.
 7. Solar-constant and solar-distribution work, begun in 1902. *Annals*, vol. 2, pp. 2, 3, 21-82, 211-228, 1908.
 8. Mount Wilson expeditions, begun 1905. *Annals*, vol. 2, pp. 7, 83-116, 1908.
 9. Theory of atmospheric transmission. *Annals*, vol. 2, pp. 13-17, 1908.
 10. Methods for measuring the solar constant. *Annals*, vol. 2, pp. 17, 57, 117-124, 1908.
 11. Transmission of the spectrobolometer. *Annals*, vol. 2, pp. 24, 51, 52, 1908.
 12. Pyrheliometry. *Annals*, vol. 2, pp. 34-49, 1908; vol. 3, pp. 47-72, 1913; vol. 7, pp. 21-23, 1954.
 13. Details of solar-constant observing. *Annals*, vol. 3, pp. 21-29, 1913; vol. 6, pp. 43-81, 1942.
 14. Sources of error in solar-constant work. *Annals*, vol. 2, pp. 58-82, 1908; vol. 4, pp. 161-176, 1922; vol. 5, pp. 110-131, 1932; vol. 6, pp. 33-42, 1942.
 15. Solar-constant results of stations compared. *Annals*, vol. 2, pp. 85-98, 1908; vol. 3, p. 134, 1913; vol. 4, pp. 177-182, 1922; vol. 5, pp. 244-245, 1932; vol. 6, p. 163, 1942.
 16. Normal solar-energy curves. Preferred determination. *Annals*, vol. 2, pp. 104-106, 1908.
Smithsonian Misc. Coll., vol. 74, No. 7, 1923.
 17. Sun's temperature. *Annals*, vol. 2, pp. 106-107, 1908; vol. 3, pp. 194-201, 1913.
 18. Atmospheric transmission, many stations, sea level up to 14,000 feet altitude. *Annals*, vol. 2, pp. 96-98, 110-112, 1908; vol. 3, pp. 104-113, 1913; vol. 4, pp. 131-158, 1922; vol. 5, pp. 168-193, 1932; vol. 7, pp. 95-98, 1954.
 19. Theory of vacuum bolometer, corrected later. *Annals*, vol. 4, pp. 45-64, 1922; vol. 5, pp. 75-81, 1932.

20. Infrared and ultraviolet corrections for solar-constant work. *Annals*, vol. 5, pp. 103-110, 1932.
21. Solar variation:
 - a. First suspected. *Astrophys. Journ.*, vol. 19, p. 305, June 1904.
Annals, vol. 2, pp. 98-103, 117-179, 1908.
 - b. Clayton's contributions. *Annals*, vol. 4, pp. 36, 185, 367-374, 1922.
 - c. From solar-constant work 1920-1930. *Annals*, vol. 5, pp. 246-269, 1932.
 - d. Short up and down trends and (1) temperatures, (2) ionosphere. (1) *Smithsonian Misc. Coll.*, vol. 95, Nos. 12 and 15, 1936; (2) vol. 104, No. 13, 1945.
 - e. Accompanying (1) hurricanes, (2) magnetic storms. (1) *Smithsonian Misc. Coll.*, vol. 110, No. 1, and (2) No. 6, 1948.
 - f. Accompanying sunspots. *Smithsonian Misc. Coll.*, vol. 110, No. 6, 1948.
Annals, vol. 7, pp. 165-168, 1954.
 - g. Periodic—(1) 27-day, (2) 6.6485-day. (1) *Smithsonian Misc. Coll.*, vol. 104, No. 3, 1944; vol. 116, No. 4, 1951; (2) vol. 111, No. 13, 1949.
 - h. Long periodic and weather. *Smithsonian Misc. Coll.*, vol. 122, No. 4, 1953.
22. A large family of periodic variations:
 - a. In the sun. *Smithsonian Misc. Coll.*, vol. 122, No. 4, 1953.
 - b. In the weather. *Smithsonian Misc. Coll.*, vol. 128, No. 4, 1955.
Smithsonian Misc. Coll., vol. 128, No. 3, 1955.
23. Defense of our solar-constant value (Abbot, Fowle, Aldrich). *Annals*, vol. 4, pp. 323-366, 1922.
24. Brightness of the night sky. *Astron. Journ.*, vol. 27, No. 3, pp. 17-24, June 20, 1911.
25. Direct and scattered radiation of sun and stars. *Astron. Journ.*, vol. 28, No. 16, pp. 129-135, March 1914.
26. Tower telescope on Mount Wilson and solar-drift curves. *Annals*, vol. 4, pp. 217-257, 1922.
Smithsonian Misc. Coll., vol. 78, No. 5, 1926.
27. Nature of the sun's sharp boundary. *Scientia*, vol. 19, pp. 171-181, March 1916.
(See also Abbot, C. G., "The Sun," 1911.)
28. Volcanoes and climate. *Smithsonian Misc. Coll.*, vol. 60, No. 29, 1913; vol. 65, No. 9, 1916.
29. Summary of the work of the Astrophysical Observatory, 1890-1920. *Annals*, vol. 5, pp. 1-5, 1932.
30. Radiometer measurements of stellar-energy spectra. *Astrophys. Journ.*, vol. 50, pp. 87-107, 1924.
Astrophys. Journ., vol. 69, pp. 293-311, 1929.

31. Campaign of observations of solar intensity on surfaces of different orientations and with various spectral regions, made at army camps for Quartermaster Corps, for a period of 8 years. *Annals*, vol. 7, pp. 144-164, 1954.
32. Daily solar-constant values, 1920-1952, with 10-day and monthly means. *Annals*, vol. 5, pp. 177-182, 1932; vol. 6, pp. 85-162, 169-175, 1942; vol. 7, pp. 26-94, 1954.
33. Convenient table for solar-constant tabulations. 10-day and monthly mean excesses over 1.900 in hundredths percentages of 1.94. Thus 1.950 becomes

$$\frac{1.950-1.900}{1.94} \times 100 = 2.58.$$

Similarly 1.940 becomes 2.06. This difference, 0.52, is 0.53 percent of mean solar constant.

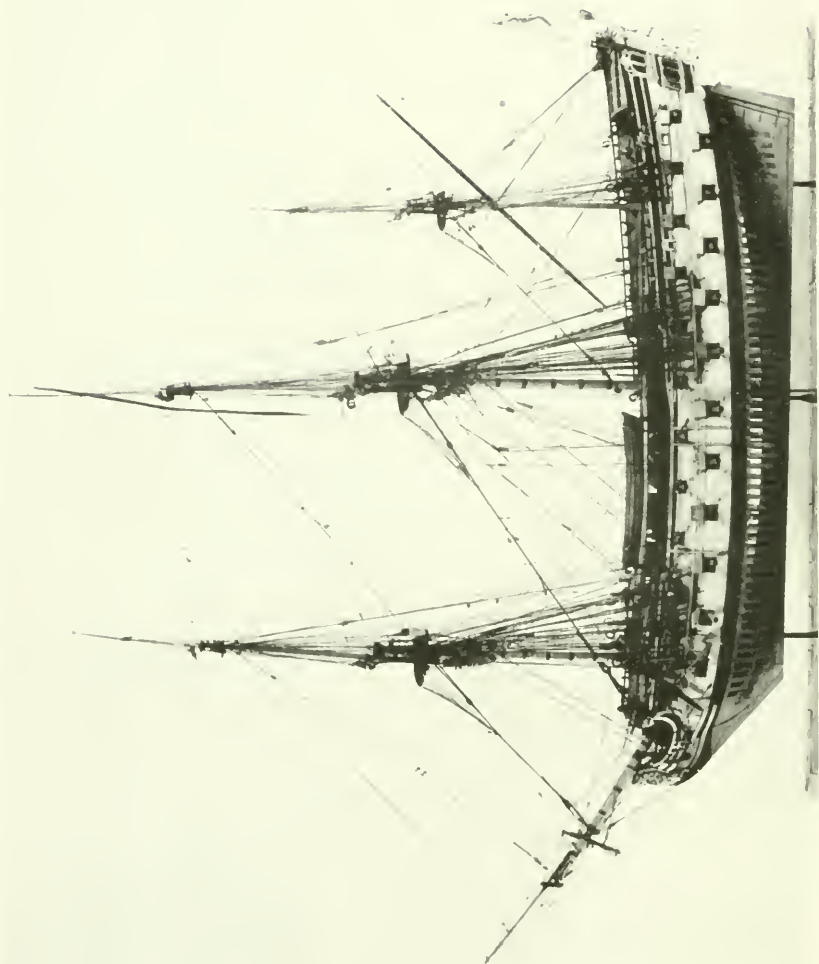
NOTE.—The tables in the two references cited above are printed without the decimal point for economy, and do not correspond with the descriptions above unless this fact is known.

PART 2.—*Work of specialists*

1. L. B. Aldrich:
 - a. The melikeron, an approximately black-body pyranometer. *Smithsonian Misc. Coll.*, vol. 72, No. 13, 1922.
 - b. Reflecting power of clouds, and earth's albedo. *Annals*, vol. 4, pp. 375-381, 1922.
 - c. Eclipse expedition, June 1918. *Smithsonian Misc. Coll.*, vol. 69, No. 9, 1919.
 - d. A study of body radiation. *Smithsonian Misc. Coll.*, vol. 81, No. 6, 1928.
 - e. Sunspots and the solar constant. *Annals*, vol. 7, pp. 165-168, 1954.
 - f. Various researches on long-wave rays. *Annals*, vol. 4, pp. 287-299, 1922.
 - g. Author (with W. H. Hoover) of volume 7 of *Annals of the Astrophysical Observatory*. *Annals*, vol. 7, 1954.
2. F. E. Fowle:
 - a. On atmospheric precipitable water. *Astrophys. Journ.*, vol. 35, p. 149, 1912.

- b. On Avogadro's number. Astrophys. Journ., vol. 40, p. 435, 1914.
 - c. On atmospheric ozone. Smithsonian Misc. Coll., vol. 81, No. 11, 1929.
 - d. On water-vapor absorption above 3 microns. Annals, vol. 3, pp. 171-193, 1913.
 - e. On water-vapor absorption below 3 microns. Annals, vol. 4, pp. 274-287, 1922.
 - f. Preparation of Physical Tables. Smithsonian Physical Tables, 5th ed., 1910; 6th ed., 1914; 7th ed., 1919; 8th ed., 1934.
3. W. H. Hoover:
- Besides his large part in volume 7 of the Annals of the Astrophysical Observatory, as coauthor with L. B. Aldrich, he engaged in classic researches on photosynthesis as a member of the staff of the Division of Radiation and Organisms, later a branch of the Astrophysical Observatory.
- a. Carbon-dioxide assimilation in a higher plant (with Earl S. Johnston and F. S. Brackett). Smithsonian Misc. Coll., vol. 87, No. 16, pp. 1-19, January 16, 1933.
 - b. The dependence of carbon-dioxide assimilation in a higher plant on wavelength of radiation. Smithsonian Misc. Coll., vol. 95, No. 21, pp. 1-13, February 27, 1937.
 - c. Improvements in use of standard water-flow pyrheliometer, and in silver-disk pyrheliometer. Smithsonian Misc. Coll., vol. 122, No. 5, pp. 1-10, August 14, 1953.
Annals, vol. 7, pp. 99-104, 1954.
 - d. Special studies of global sun and sky radiation (with L. B. Aldrich). Annals, vol. 7, pp. 144-164, 1954.
 - e. Mechanical integrator for Brown recording potentiometer. Annals, vol. 7, pp. 138-139, 1954.





Model of a British 50-gun ship of about 1710. The *Loo* was very similar to this type although slightly smaller. There are no existing models or pictures of a ship of the same class as the *Loo*. (Photograph from the Naval Museum, Greenwich, England.)

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 131, NUMBER 2

THE LAST CRUISE OF H.M.S. "LOO"

(WITH 17 PLATES)

By
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Smithsonian Institution



(PUBLICATION 4224)

CITY OF WASHINGTON
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(WITH 17 PLATES)

In the spring of 1951 I was invited by Dr. and Mrs. George Crile, Jr., of Cleveland, Ohio, to accompany them on an expedition to explore remains of a ship that had been wrecked about 5 miles off the main line of the Florida Keys over two centuries ago. The wreck had been shown to them by William Thompson, of Marathon, Fla. Only one thing was known about the ship—that it went down sometime after the year 1720. This was indicated by the fact that in 1950 Dr. and Mrs. Crile and their party had recovered some copper coins from the site, one of which was a Swedish half-ore piece (pl. 2, fig. 1) dated 1720. The site was a reef named "Looe" on the charts and was located some 25 miles southwest of Marathon. At the time, the source of the name was unknown, and its presence on the charts was not considered significant.

On Sunday evening, May 27, most of the members of the expedition assembled in Miami, and the next day left for the Keys and Thompson's yacht harbor, which was to be the base of operations. Here the entire party came together. It consisted of the sponsors, Dr. and Mrs. Crile; Mr. and Mrs. E. A. Link, of Binghamton, N. Y.,¹ Mr. and Mrs. James Rand, of Cleveland, Ohio; Mr. and Mrs. John Shaheen, of New York City; William Thompson, of Marathon, Fla.; Arthur McKee, of Homestead, Fla., an experienced diver on shipwreck sites; and myself. Necessary supplies and equipment were assembled and tested, and the boats were made ready. We were to use a barge built on a Higgins boat hull, a small fishing launch, and later Mr. Link's yawl, the *Blue Heron*.

Early Wednesday morning, May 30, the party left for the reefs

¹ The participation of Mr. and Mrs. Link in the expedition was to prove very fortunate for the National Museum since it led to the establishment of the Link Fund through their generosity. This fund enables the Museum to participate in annual expeditions to explore historic wreck sites in the Florida Straits area.

and by midmorning were over the wreck site (pl. 3). To locate the wreck exactly it was necessary to get into the water with face plates and carefully scan the sand bottom of a "valley" lying between two fingers of the reef which ran out to sea. Only the metal objects from the ship remained, and these were covered with a sand crust giving them the same color as the bottom—excellent camouflage, which made them almost invisible from the surface of the water. We detected the outlines of bars of metal, the ring of one of the ship's anchors (pl. 4) jutting from the reef, two long cylindrical objects, encased in marine growths, which were recognized as guns from the ship, and, upon closer inspection, piles of round objects encrusted with sand—solid shot for the ship's guns.

After a preliminary survey from the surface, the boats were pulled over the wreck and the diving gear was prepared for operation. Tight-fitting rubber masks that completely covered the face were connected to the air compressors by long lengths of strong rubber hose. The divers strapped on their lead belts, put on their masks or helmets, and went over the side on the diving ladder and lifeline.

The first object recovered was a large chunk of metal roughly triangular in cross section and stepped on the surface. It proved to be solid cast iron and was identified as permanent iron ballast cast to fit along the keelson of the ship. Clinging to it was a solid iron shot $3\frac{1}{2}$ inches in diameter, a standard 6-pound shot of the eighteenth century. These finds immediately revealed two additional facts concerning the ship—she was most probably a warship, since merchantmen carried disposable ballast of stone, and she had 6-pounder guns in her batteries.

The next day the attention of the divers was devoted to the smaller objects lying about in the sand "potholes" on the site. By the use of a powerful jet of water the sand was carefully washed away and the articles were uncovered (pl. 5). Soon basketfuls of sand-encrusted hull bolts, nails, solid iron shot, fragments of rum or brandy bottles, Chinese porcelain dishes, and earthenware, and many other objects were being emptied on the decks of the salvage boats. On the first of two brief dives that the author made on the site a basketful of solid iron shot was gathered (pl. 6). In this lot was found a 6-pound shot with an arrow on it, which was immediately identified as the broad arrow (pl. 7). This was the first indication of the nationality of the ship, as this symbol has been used for centuries by the kings of England and Great Britain to mark royal property. The occurrence of the broad arrow on the shot was not conclusive evidence that the ship had been British, since ordnance stores could have been captured

or stolen by the enemies of Britain. But until further evidence proved the contrary, we could consider the ship to have been British.² In the basket 12-pound, 1-pound, and $\frac{1}{2}$ -pound shot were also found, giving additional information on the ship's batteries. The broad arrow also appeared on the 12-pound shot.

On Thursday, May 31, and Friday, June 1, numerous small objects were brought up, including more porcelain fragments, parts of clay pipes and rum bottles, the wooden knob of a walking stick, the eye-piece of a navigation instrument, pieces of stoneware decorated with blue flowers, and animal bones (later identified as pig and cow) from the pickled-meat stores of the ship. (See pls. 8, 9, and 10.)

On Saturday, June 2, the party remained ashore to sort, clean, and begin the preservation process on the objects recovered. Fragments of wood were packed in fresh water for shipment to the National Museum, the sand crust was cleaned from the cast-iron and other large iron objects by light hammering, and the objects were placed in baths of fresh water to leach out the sea salts.

The cast iron was found to have been oxidized to a depth of one-half to three-fourths of an inch. The removal of the sand crust from all surfaces (those portions having been converted to crystalline magnetite, which was very friable) had to be done with great care. The porous oxidized layer was saturated with chlorides, and to break these down the cleaned shot were placed in baths of sodium hydroxide. Most of the shot were packed with the sand crust on them, the crust protecting them from excessive drying while on the way to the Museum.

On Sunday and Monday (June 3 and 4) a continual stream of material came up from the wreck and was added to the piles ashore at our base (pls. 11, 12). There was such a quantity of specimens that it was decided that the author should devote a full day to identifying, sorting, cleaning, and preserving those that were to be retained. The boats went out as usual and that evening returned with one of the cannon barrels. Mr. Link had rigged the main boom of the *Blue Heron* and had lifted it to her side with block and tackle (pls. 13, 14). Through skillful seamanship and favorable weather the 2,000-pound barrel was brought to Marathon, hanging beside the delicate mahogany hull of the yawl, which was protected with rope fenders. As soon as the barrel was on the ground at our base we began removing the sand crust with a hammer. As the crust fell away (pl. 15)

² Later a chain plate, which was originally bolted to the ship's hull, was found by a salvage party from Miami. It also bore the broad arrow.

the beautifully molded contours of an eighteenth-century barrel were revealed (pl. 16). The appearance was deceptive, however, for while the physical form of the barrel was perfect it was evident that the surface of the iron had been oxidized deeply.

Two more clues to the identity of the ship were furnished by the barrel. On the second reinforce over the trunnions was a crowned rose, and in the muzzle were the remains of a wooden tompon. The crowned rose was an insigne employed by the Tudor and Stuart monarchs of England and was not used as the principal mark on royal artillery after the death of Queen Anne in 1714. The fact that the tompon was in the barrel indicated that the ship had run aground through accident or storm and not as an aftermath to a naval engagement. The crowned rose enabled us to estimate the date before which the ship sank. Since the normal life of an iron barrel on shipboard was usually not over 35 or 40 years, the barrel had probably not been in active service after 1714 plus 35 or 40 years, or 1749-1754. It was therefore assumed that the ship must have sunk before the year 1750.

The barrel was the last important object recovered from the wreck site in 1951, and we now had all the evidence that we could expect to recover that year. This evidence had told us that the ship was a British warship, had sunk between 1720 and 1750, had 6- and 12-pounders in her main battery, and had gone down as the result of an accident and not as a sequel to a naval action. We knew, of course, that the reef on which the ship had sunk was called "Looe Reef," but we had not suspected a connection between the name and the wreck itself.

After my return to Washington I began a search of the ship casualty lists for the eighteenth century published in Clowes "The Royal Navy," and found the entry—"1743 *Looe* 44 guns, Capt. Ashby Utting, Lost in America." Further research indicated that she carried 6- and 12-pounders. The conclusion was obvious—the ship we had investigated was the *Loo* whose wreck had given her name to the reef. That night I phoned Dr. and Mrs. Crile in Cleveland and they immediately called a friend in London. Within a week the Public Record Office had yielded a letter written by Captain Utting at Port Royal, S. C., February 15, 1743/44,⁸ in which he described the wreck of his ship. A year later I was in London digging out all the documents in the Public Record Office relating to the ship. The account that follows is based on letters, the Navy List, the *Loo*'s pay lists and muster

⁸ The legal year began March 15. The calendar year was 1744. (See Appendix B for Utting's letter.)

rolls and other documents in the Public Record Office in London. All these documents are Admiralty papers. The references are given in the manner in which they are numbered in the collections of the Public Record Office, and bear the prefix ADM or AD.

On June 14, 1743, Thomas Corbett, Secretary of the Admiralty, sat down in his London office and countersigned an order directing Capt. Ashby Utting to prepare his ship, the frigate *Loo*,⁴ for a cruise to North America:

Having order'd His Majesty's ship under your command to be refitted at Portsmouth, for a voyage to North America, cleaned, sheathed and graved,⁵ and her provisions compleated to six months of all species, except beer, and of that as much as she can conveniently stow, and stored accordingly; you are hereby required and directed, to repair with her into Portsmouth Harbour, and strictly to observe the following instructions.

You are to give constant attendance.

W: IC: GL:⁶

By T.C.

Thus began the last cruise of the *Loo*, the story of which might have been taken from a classic work of fiction.

The *Loo*, a frigate of 40 to 44 guns, had seen long service in the Royal Navy. She had been built during the expansion of the British fleet incident to the War of the Spanish Succession. In this war England was fighting to prevent the seating of a Bourbon⁷ on the throne of Spain—a scheme of Louis XIV to strengthen the position of France in Europe. The *Loo* was to meet her end during another war in which Spain and Great Britain were enemies, a war that began as a result of the succession of Maria Teresa to the throne of Austria.

⁴ Named for the old seaport town of Looe (also Loo), which lies on the rocky coast of Cornwall and which has supplied sturdy sailors to the Royal Navy since its beginning.

⁵ The first Royal Navy vessel to be sheathed with lead was the *Phoenix*; this was done in 1670. The practice had been followed in the Spanish Navy since the middle of the sixteenth century and in some cases by English merchant ships (see Clowes, *The Royal Navy*, vol. 2, p. 240). Lead proved impractical, however, and the practice of sheathing with thin fir boards was followed until the time of the American Revolution, when the British fleet was sheathed with copper. The thin fir sheathing was backed with pitch and horseshair, which discouraged worms from tunneling into the ship's planking. Graving was the process of burning sea life from the bottom of a ship.

⁶ Initials of the Lords of the Admiralty, "W" for Daniel, Earl of Winchelsea, First Lord of the Admiralty, March 19, 1742, to December, 1744. "T.C." for Thomas Corbett, Secretary of the Admiralty, 1742-1751. (Admiralty Out-Letters, ADM 2, vol. 60, p. 15, Public Record Office.)

⁷ The grandson of Louis XIV, who ruled as Philip V of Spain (1700-1746).

She was most probably launched in 1706⁸ since she first appears in the Navy List under the date April 1, 1707, when she was at "Long-reach taking in Guns."⁹ Her complement at that time is given as 190 men and her battery as 42 guns.

The Navy List thereafter follows her career in terse monthly entries (see Appendix A).

Her first two cruises carried her to Archangel and Newfoundland.¹⁰ By 1709 she was back at Sheerness refitting, and afterward was on patrol duty in the Channel.¹¹ Early in 1710 she was attached to the Dunkirke Squadron and in the fall of that year was on convoy duty to the eastern countries.¹² In April 1711 she was in Holland "to bring the Queen's wine to the Nore."¹³ She then sailed convoy to Russia and during the last two months of 1711 was refitted and again sent to duty in British waters, meeting ships from Virginia and convoying them to British ports.¹⁴ During the winter of 1712-13 she transported troops to Bayonne and returned with prisoners of war¹⁵ and then again served in the Channel, cruising against smugglers.¹⁶ In the fall of 1714 she was sent convoy to Port Mahon in the Mediterranean and on return was paid off and laid up.¹⁷

Three years later the *Loo* was back in service as a hospital ship on duty with the Baltic Squadron.¹⁸ She was then laid up for the winter and the next spring again commissioned as a hospital ship and sent to the Mediterranean Squadron. A year later (April 1719) she appears in the Navy List with 30 guns and a crew of 125 men, which probably indicates that she had been reconverted to a frigate.¹⁹ Thus fitted out she served with the Mediterranean Squadron until the spring of 1722.²⁰ From that time until January 1728 she appears to have been laid up. On January 10, 1728, she was again in sea pay and until

⁸ At least one earlier *Loo* is recorded. Like her successor, she was a frigate of 40 guns and was also lost through shipwreck, having run aground on the Irish coast near Baltimore, April 30, 1697 (Clowes, *The Royal Navy*, vol. 2, p. 536).

⁹ Navy List, Jan. 1, 1707-Dec. 31, 1709, ADM 8/10, Public Record Office.

¹⁰ ADM 8/10.

¹¹ *Ibid.*

¹² *Ibid.*

¹³ *Ibid.*

¹⁴ ADM 8/10 and 8/11.

¹⁵ ADM 8/11.

¹⁶ ADM 8/12.

¹⁷ *Ibid.*

¹⁸ ADM 8/13.

¹⁹ *Ibid.*

²⁰ *Ibid.*

July 1730 was on duty in British waters performing such tasks as transporting clerks and money to the pay at Plymouth and patrolling the Channel.²¹ In August she was ordered to the Mediterranean as convoy for transports going to Gibraltar and remained in the Mediterranean cruising against the Barbary pirates "on the Coast of Sallee."²²

Coming home to Britain in August 1731, the *Loo* was again on Channel service until the next spring.²³ For three years she was again laid up and on May 5, 1735, was commissioned and fitted out as a hospital ship for duty in the Channel service. In August of that year she joined the naval forces at Lisbon, still as a hospital ship, and served there until the spring of 1737.²⁴ From that time until January 1742 she was laid up and, war having broken out between Great Britain and Spain, was recommissioned as a frigate of 44 guns on January 5 and placed in the Channel service under the command of the Earl of Northesk. While on a cruise in the area of Cape Finisterre (northwest Spain) the *Loo*, in company with the *Dealcastle* (24 guns) raided Vigo Bay, capturing four Spanish vessels in the harbor, an incident reported in the *London Gazette* for August 31, 1742.²⁵

²¹ Ibid.

²² Ibid.

²³ ADM 8/17 and 8/18.

²⁴ ADM 8/19 and 8/20.

²⁵ Also mentioned in the *Gentlemen's Magazine* for August 1742, p. 445, and September 1742, p. 494, giving an account of the *Loo* raiding in the Porto Nova and Santiago areas: "The Earl of Northesk, Capt. of his Majesty's ship the *Loo*, being on a cruize off of Cape Finisterre, and the parts adjacent, received intelligence of a small Privateer being at Porto Nova, upon which he stood in there on the 30th of June, but the Privateer discovering him, got higher up the river than the *Loo* could venture, and it falling calm, Ld. Northesk was obliged to anchor close by the towns of Porto Nova, and St. Iago, into which he fired a few shot, then landed some men and dismounted 4 guns which were on a battery at Porto Nova, and set fire to several houses at St. Iago. On July 7, Lord Northesk met with his Majesty's Ship the *Dealcastle*, commanded by Capt. Elton, and receiving intelligence of some vessels being at Vigo, they run up the river and anchored before that town, where they made prizes of 4 vessels, 2 of which they set on fire, being light, and not having Sails on board to bring them out. They fired several shot into the Town to cover the boats while they cut away the vessels, there being a pretty smart fire at them with small arms from the shore. On July 19, upon intelligence that the privateer was still about the river of Porto Nova, the *Loo* run in and anchored under the Island of Blydones, where Lord Northesk put a Lieutenant and 60 men, with 2 of the ship's 6 Pounds, into a Sloop taken at Vigo, and sent her up the river in quest of the privateer; the Sloop could see nothing of her, but in her return chased a bark on shore, and set her on fire; and Lord Northesk landed some men, and burnt a village of about 40 houses."

Following this cruise, the *Loo* was again in the Channel service until May 1743, when she was ordered "To cruize between Bilbao and St. Jean de Luz,²⁶ to intercept some Caracca ships²⁷ expected at St. Sebastian."²⁸ At the conclusion of this cruise, which lasted some six weeks, the *Loo* returned to Portsmouth to refit for her ill-fated voyage to North America. Meanwhile Capt. Ashby Utting had assumed command under a commission dated 4 April, 1743.²⁹ As the war between Great Britain and Spain had progressed, the people of the infant colonies of Georgia and South Carolina had felt increasing fears of an invasion by the Spanish from Florida and Cuba. In 1742 the Spanish had attacked Fort Frederica in Georgia but had been repulsed by the troops of General Oglethorpe at the Battle of Bloody Marsh. After this attempt by the Spanish the colonists felt that the threat of devastation of their homes and farms was even greater. Consequently, the Lords of the Plantations in London had been petitioned by the Governor of South Carolina to send a large warship to the Carolinas for the protection of the coastline. The result was the ordering of the *Loo* to the Charleston station.

Three days after Secretary Corbett signed the *Loo*'s orders Captain Utting had received them and replied that he would "punctually comply" with them and use his "utmost endeavours" to get his ship ready for sea.³⁰ The *Loo* sailed soon after Utting's letter was posted and arrived at Portsmouth on the morning of June 18. Reporting his arrival there to the Secretary of the Admiralty, Utting complained that the 6-pounders³¹ on the upper deck of the *Loo* were "very indifferent and not fitt for a forrain voyage, being much honey combed."³² a fact made known to him by his gunner, Samuel Kirk.³³ Utting recommended that a battery of 9-pounders, which had been mounted for the *Hunnington*, be substituted for the *Loo*'s worn-out 6-pounders.³⁴

²⁶ On the northern coast of Spain.

²⁷ That is, ships of the Caracas (Venezuela) Company.

²⁸ ADM 8/23.

²⁹ Commission and Warrant Book, 1743-1745, AD 6/16, p. 335.

³⁰ Admiralty In-Letters, ADM 1, vol. 2625, pt. 3, No. 146.

³¹ Heavy guns of this period were rated by the weight of the solid shot they threw. The barrel of a long 6-pounder of this period weighed around 2,000 pounds.

³² That is, the barrels, which were cast iron, had small cracks in their bores.

³³ Kirk's name is mentioned in the record of the Court Martial of Captain Utting held May 3, 1744 (Admiralty In-Letters, ADM 1, vol. 5283).

³⁴ ADM 1, No. 417. Utting's recommendations were not followed. This is proved by the finding of the same 6-pounders on the wreck site of the *Loo*. They

Preparations for the cruise proceeded swiftly. On June 20, the day after Utting wrote his letter concerning the guns, the Admiralty ordered the Captain to "make out" his pay books "to the 30 June, 1742."³⁵ Five days later admiralty orders "about carrying candles up and down the ship and drawing off spiritous liquors and an order to cause the men's allowance of rum to be diluted with water when in the West Indies" were issued.³⁶ The order directed that "whenever the ship's Company under your command are served with Rum, Brandy, or any other spirituous liquor, instead of Beer, the same be constantly issued out to them by the Purser upon the open Deck, and nowhere else; and that you do order all officers and others under your command, never to draw off any arrack,³⁷ rum, brandy, or other spirituous liquors in places under deck, but always upon open deck."³⁸

bore the crowned rose, a device placed on royal guns during the reigns of the Tudors and the Stuarts. The *Loo's* 6-pounders were therefore cast before the death of Queen Anne in 1714. Thus they would have been at least 30 years old at the time of the loss of the *Loo*—a fact borne out by Utting's statement on their condition.

³⁵ ADM 2, vol. 60, p. 34. A year's delay in paying the men was a common (even usual) occurrence at this time.

³⁶ *Ibid.*, p. 41. These orders stemmed from the loss of the *Tilbury*, 60 guns, in the West Indies through fire on September 21, 1742. The incident was reported by Adm. Edward Vernon in a letter to Thomas Corbett written on the flagship *Boyne* in Port Royal harbor, Jamaica, October 3, 1742 (Admiralty In-Letters, ADM 1, vol. 233, extracts.) "I am heartily concerned for the melancolly account lately brought me by Captain Lawrence late of the *Tilbury*, who came in here the 24 September in the Island Sloop, with part of his officers and men, another part remaining on board the *Defyance*, in execution of my orders, and upwards of a hundred of them having perished in the sea or fyre, on her accidentally taking fyre, and burning, and sinking in the sea, amongst which are the Master, Boatswain, and Gunner, and a Marine Officer. But I cant proceed to enquire in it at a Court Martial, til the return of the *Defyance*, many evidences that saw the first of it, being absent in the *Defyance*, so all I can say of it at present is, that it took its rise from a Marine soldier's snatching to get a bottle rum, out of the Purser's boys hand, who had a candle in the other hand, declaring he would have a dram, and in the struggle with the boy, the bottle falling and breaking, and the candle with it the rum took fire, and communicating to more in the Pursers cabbin where the fyre first began, that could not be extinguished by all their diligence afterwards, tho they say, they threw all their powder into the sea." Admiral Vernon at the same time submitted a copy of a general order he had published to his forces two years before requiring that the rum ration be served to the men on deck, and that it be diluted with water. The new concoction became known as "grog" after Admiral Vernon who was called "Old Grog" from his habit of wearing a "grogram" cloak. "Grogram" was a coarse material of silk and mohair. The name is derived from "gros-grain."

³⁷ A drink distilled from rum.

³⁸ Admiralty Out-Letters, ADM 2, vol. 59, p. 380.

Another order dated the same day directed Utting to have his ship "vichialled to four months only ³⁹ for a forreign voyage, and what beer she cannot take in to be made up with good brandy . . . and to cause half of one and half of the other to be issued." It also instructed Utting to load the food as quickly as possible and "to take care, that the brandy supplied . . . be good and wholesome," and to report to the Lords of the Admiralty "the usefullness of the allowance of half brandy and half beer and what effect it has upon the health of the men." ⁴⁰ Utting silently conformed with these orders as they were received, but on July 2, still hoping to receive the battery of 9-pounders to replace his wornout 6's, he wrote: "The time for taken in my guns draws very near, and ye officers of ye ordinance here has no orders concerning ye 9 pounders, which I had wrote for and was in hopes I should have had them as ye ship would well bare them and make her a much better man of war." ⁴¹ He also requested that, if possible, he be told his ultimate destination since he knew only that he was to go to North America.

On July 11 orders were issued to the commanding officers of the *Rye*, 20 guns; *Flamborough*, 20 guns, and the sloop *Spy*, 8 carriage guns and 12 swivels, all stationed in South Carolina, to place themselves under the command of Captain Utting upon his arrival there. Utting was to carry these orders with him.⁴² The next day the Admiralty issued instructions to Utting concerning the impressment of seamen while in America, furnishing him with three press warrants. The instructions cautioned him that "it is not meant, that the trade of His Maj's. subjects in America, or ships provided with Letters of Marque to cruise against the Enemy should be distressed thereby, but only that such prudent use be made of the said press warrants as may enable you to procure men to make up your complement, when proper opportunities offer it. You are to take great care, that no indiscreet or unreasonable use be made of them." The instructions also directed that Utting was "never to molest the chief officers, such as the master, mate, boatswain or carpenter, or any seaman found on board with protections granted by us, pursuant to Act of Parliament." ⁴³

³⁹ Thus rescinding the order of June 14, which had directed the loading of a 6-months' supply of food.

⁴⁰ Admiralty Out-Letters, ADM 2, vol. 60, p. 42. Beer had been a standard beverage in the English Navy since earliest times. Easy to keep, it was superior to water, which grew putrid in the casks.

⁴¹ ADM 1, vol. 2625, pt. 3, No. 418.

⁴² ADM 2, vol. 60, p. 79.

⁴³ Ibid., p. 80.

The same day detailed orders covering all phases of the cruise to North America were issued. They are an excellent example of the type of orders of that period given to senior officers destined for independent duty in remote parts of the Empire, and they are here quoted in their entirety.⁴⁴

TO CARRY GOVERNOR CLINTON TO NEW YORK AND THEN
ATTEND ON SO. CAROLINA

Whereas we have appointed His Maj's. ship under your command to carry the Hon. Geo. Clinton, Esq. to his Government at New York, and then to attend on the Colony of South Carolina, you are hereby required and directed to make all possible dispatch in getting her compleated in all respects for the Sea, and you are to receive on board the said Mr. Clinton, with his Family and Equipage, and give them passage to New York, vichialling them as your Ship's Company during their continuance on board, and allowing the Governor all such accommodation as the Ship will afford.

And whereas the ship under your command is only ordered to be vichialled to four months, and to have two months French Brandy instead of two months beer; and the Comrs. of the Vichialling having a large quantity of Brandy in store at Guernsey, in the Charge of Mr. Nich S. Dobree, a merchant in that Island, you are in your way down the Channel, to call off of Guernsey, without going into the Port, and send the enclosed letter with your Purser on Shore to the said Mr. Dobree; and receive from him such a quantity of Brandy as you think necessary for the use of your Ship's Company and you can conveniently receive on board, which when you have done, you are to proceed directly to New York, without touching at the Madeiras, and there land the Governor, with his Family and Equipage; and having so done, you are to proceed on to South Carolina.

And whereas His Maj's Ships the Rye, Flamborough, and Spy Sloop, are stationed at South Carolina, You are to take them under your command, their Captains being directed to follow and observe your orders.

When you arrive at South Carolina, you are to communicate these our instructions to the Governor and Council of that Province, and to consult and advise with them from time to time, in what manner the ships under your command may be best employed in guarding the coasts, and securing the trade of that colony from any attempts of the Enemy, and to govern yourself according as shall be agreed on, using your best endeavors to take or destroy all such ships or vessels of the enemy, as shall come upon the coasts of the said Colony.

And whereas it has been represented to us, that the Coast of North Carolina is very much infested with Spanish Privateers, who have even landed in the Country and carried off hogs and black cattle, to the great terror of the inhabitants of those parts, you are, when you see proper occasions, to extend your cruize as far as Cape Hatteras, or to order one of the ships under your Command to do so, for the better protection of the trade of His Maj's. Subjects in those parts; and you are to acquaint the Governor of North Carolina with this part of our instructions.

⁴⁴ Admiralty Out-Letters, ADM 2, vol. 60, pp. 81-84.

And whereas it has been represented to us, that the Town of St. Augustine depends much upon what comes by Sea for provisions, and would be greatly distressed, if His Maj's. ships stationed at Carolina would sometimes cruize off that Port, to prevent provisions being carried to that place by Sea, you are to have a particular regard to that service, as far as may be consistent with the other necessary services on which you may be employed.

And whereas we have directed the Captains of His Maj's. ships attending on Virginia to hold a constant correspondence with you, you are, whenever you shall find the Enemy's ships to be too strong for you, to send immediate advice thereof to the Captains of the said ships, whom we have directed to repair to your assistance, and you are to endeavour joyntly to take or destroy them. And if the Captains of the said Ships shall at any time send you notice of the Enemy being too strong for them, you are with all possible diligence to proceed to their assistance, communicating in the first place the intelligence you have received to the Governor and Council of South Carolina, and receiving their concurrence for your so doing, and when the service is performed, you are to return to your station.

And whereas the Captains of His Maj's. ships stationed in America, have of late years taken a very unwarrantable Liberty of lying in Port with their Ships, for the greatest part of the time they have remained abroad, to the dishonour of His Maj's. service, and the disservice of the Colonies for whose protection they are appointed, and we being determined not to suffer any such neglect for the future, do hereby strictly charge and direct you to keep constantly at Sea, when the weather will permit, and cruize in proper stations for meeting with the Enemies ships or privateers, and for protecting the trade of His Maj's. subjects, and guarding the said colony of Carolina from any attempts of the Enemy.

You are not to fail to transmit to us, one in every two months an exact copy of the Journal, that it may be seen what care and diligence you have used in putting our instructions in execution and to order the Captains of His Maj's ships under your command to do the same.

And in order to enable you the better to keep the ships under your command in a good condition to cruize and protect the trade, as well as to annoy the Enemy, you are to cause them to be cleaned once in six months, at such times as it can be most conveniently done.

When the ships you command are in want of provisions, you are to apply to the Contractors of the victualling at Carolina, for the same, and never to leave the said Colony defenceless by going somewhere to victual; and you are to take on board no more provisions at a time, than are necessary for the service on which you are employed.

You are not to hoist the Union Flag on board the Ship you Command, on account of the Governor's being on board, or on any other pretence whatever.

In case of the death of any of the officers of the ships under your command, you are to appoint such other persons to act in their names, as by the quality of their Employments ought to succeed therein.

When you shall receive our orders to return to Great Britain, you are to take in no more provisions than shall be sufficient to compleat what you may have on board to three months of all species at whole allowance, upon the penalty of making good what damage, His Majesty may otherwise receive thereby.

You are, as you pass through the channel, to examine such ships and vessels as you shall meet with passing from Great Britain or Ireland to France, which

you shall reasonably suspect to have Wool⁴⁵ on board, and upon discovering any with that commodity in them, to send them into the nearest Port, and deliver them into the care of the Collector of the Customs, in order to their being prosecuted according to Law.

You are by all opportunities to transmit to our Secretary for our information, an account of your proceedings, and of the condition of the ships under your command as to the number of men, and all other particulars and in case of inability by sickness or otherwise, to be careful to leave these our instructions with the next Commanding Officer. Given 12th July, 1743.

W. J.C. G. L.

By
T.C.

Capt. Utting, Loo, Spithead.

Captain Utting must have received oral instructions that he was to carry Governor Clinton to New York several days before he received the above orders. In fact the Governor had either visited the ship or had otherwise instructed Captain Utting on the accommodations that he desired aboard the *Loo*. Five days before the detailed orders on the cruise were written Utting had written Corbett "the carpenter will have compleated every conveniency Mr. Clinton desires by tomorrow night . . ." ⁴⁶

On July 14 Utting acknowledged receipt of the orders of July 12 and reported that his ship was "in all respects fitt for sea." ⁴⁷ Four days later the Admiralty instructed Utting, who was now at Spithead ready to sail, to convoy the storeship *Pegasus* "laden with naval stores for New York and South Carolina" to America, ordering that he "convoy her safely to New York, where you are to cause her to be unloaden as soon as possible, and then proceed with her to South Carolina." ⁴⁸ At the same time additional instructions on cruising while in America were issued. ⁴⁹

TO CRUIZE BETWEEN CAPE FLORIDA, AND THE NORTH WEST PART OF THE GRAND BAHAMA WHEN THE SEASON OF THE YEAR WILL NOT PERMIT HIS CRUIZING OFF CAROLINA.

In addition to our instructions to you dated the 12th instant, you are hereby required and directed, when the Season of the Year is not proper for your cruising on the Coasts of South Carolina, and that neither the said Colony, nor

⁴⁵ The export of English wool was absolutely prohibited at this time in an effort to encourage the English woollen industry. The demand for English raw wool in the lowlands was great, and consequently the smuggling of it to the continent was profitable.

⁴⁶ ADM 1, vol. 2625, pt. 3, No. 419.

⁴⁷ Ibid., No. 420.

⁴⁸ ADM 2, vol. 60, p. 96.

⁴⁹ Ibid., pp. 96-97.

that of Georgia is under any apprehension of being molested by the Enemy from Havanna or Augustin, to proceed with His Maj's. Ship under your Command and Cruize between Cape Florida and the North West part of the Grand Bahama, 'til such time as the Season will permit your return to Carolina, taking care to have a sufficient quantity of provisions on board to last you on that service.

You are diligently to look out for the Enemy's ships passing through the Gulph of Florida for Europe, and use your utmost endeavours, to take, sink, burn or destroy them.

But before you proceed on this Service, you are to communicate your design to the Governor of Carolina, and not to go thereupon, if you find any reasonable objections thereto. Given 18th July, 1743.

W. J.C. B.

By

T.C.

Capt. Utting, Loo, Spithead.

Utting had been thinking of the same operations plan as that of the Lords of the Admiralty, for on July 19, a day or so before he received the additional instructions, he had written :

I was a little hurried to save post with my last yet dont know whether I explained ye plans and time of cruising so plain as you could wish for fear of which beg you'll be pleased to indulge me with this to acquaint you. I propose (if ye service will allow me and you can git me orders) to saile from South Carolina ye 10 or 15 of October and cruise in and about ye Gulfe of Florida, as far as ye Cape⁵⁰ if I can git there till ye middle of Jany. then return to Carolina. And as soon as I can water, victuall, and refitt, in all respects, then propose to saile, and cruize on ye coast of Carolina of [off] St. Augustine or on such part of ye coast as I shall find the service require me most. Given ye 20 gun ships proper stations as ye service shall require, on this coast I propose to keep all ye summer months⁵¹; ye latter end of May shall go in for 6 or 8 days to victuall and water and then cruize till ye 20 or 25th. of July when as I shall be then about 12 months foull shall go in to heave down and about ye 20th of Sepr. shall saile to cruize on ye aforesaid station: yet I never propose to be in port above 2 months in ye year; after my first careening shall heave down every 6 months. But as I am graved and tallowed⁵² can go 12 months at first. There is an exceeding good careening place at Port Royall⁵³ which can be made ours

⁵⁰ Cape Florida.

⁵¹ That is, keep to the sea during the summer months.

⁵² See footnote 5, p. 5. In navy yards graving was usually done in a drydock. On remote stations it was necessary to careen the vessel by mooring her in a river, unloading her, and then "heaving her down" by pulling her over with tackles secured to trees on the bank. In this position half of her bottom was above water and could be cleaned. The process was repeated for the other side of the bottom. Hulls were coated with tallow as a protection against growths and water penetration of the ship's planking.

⁵³ South Carolina.

conveniently to heave down without expense to the government. I have wrote to ye Navy Board for careening gear, but have not had an answer.⁵⁴

On July 25 the Captain acknowledged receipt of the further instructions on cruising and the orders to escort the *Pegasus*, and prepared to set sail.⁵⁵

On August 6 Governor Clinton, his wife and her children, and suite of 15 persons came aboard the *Loo*.⁵⁶ She probably sailed within a week.

Six weeks later the *Loo* arrived safely in New York harbor with her charges, and the *Pegasus*. The Governor and his suite disembarked on September 22.⁵⁷ Utting reported in a letter dated in New York Harbor September 29 that the voyage had been uneventful "with nothing worth their Lordships notice." In the same letter the Captain made his first report on the trial ration of half brandy and half beer, stating that it agreed with men "extreamly well, and they are well pleased."⁵⁸ The ship, he reported, was unmooring as he wrote, and expected to sail that afternoon for South Carolina escorting the *Pegasus*. His departure was delayed until October 6, however, probably by adverse weather, but the bright lights of New York might have been the real reason, since Utting mentioned no cause for the delay. After a passage of five days the *Loo* arrived off Charleston Bar. In Charleston he found the sloop *Spy* ready for sea, the *Rye* "cleaned and almost fitt for sea," the *Flamborough* "sheating."⁵⁹ He immediately delivered the Admiralty orders instructing the captains of these ships to place themselves under his command, and then issued orders giving each ship stations for cruising off the Carolina coast for the defense of the colonies and protection of English and colonial shipping. Captain Hardy of the *Rye* was directed to "cruize on the coast of South Carolina, between Charles Town Barr and the So.W most part of the same coast, keeping off St. Augustine, and as near into the shore as you shall judge proper when winds and weather will permitt to intercept any trade that may come from the Havanah to that place."⁶⁰ Hardy was also instructed to inform the Governor of

⁵⁴ ADM 1, vol. 2625, pt. 3, No. 421.

⁵⁵ Ibid.

⁵⁶ *Loo's* General Muster Book, ADM 36, Ser. I, vol. 1823.

⁵⁷ *Loo's* General Muster Book, ADM 30, Ser. I, vol. 1823.

⁵⁸ ADM 1, vol. 2625, pt. 3, No. 423.

⁵⁹ Ibid., No. 435. British ships were at this time sheathed with thin fir boards backed with horsehair and pitch. The sea worms ate through the thin board but were repulsed by the hair, and the ship's hull planking was thus protected.

⁶⁰ ADM 1, vol. 60, No. 435.

Georgia⁶¹ of his activity off that coast, to remain at sea as long as his water and provisions would permit, and, after returning to Charleston to take on supplies, to return to his station and cruise as soon as his ship was ready for sea.⁶² Captain Hamar of the *Flamborough* was directed to cruise off the coast of North Carolina. "Whereas the Rt. Hono. the Lords Commiss. of the Admiralty has been informed that the coast of North Carolina has been much infested with privateers [Spanish] to the great determent of the inhabitants of that province, you are to use your utmost endeavours to take or otherwise destroy them or any of the enemy's ships as you may possible meet with in your cruise."⁶³ Hamar was directed to inform the Governor of North Carolina⁶⁴ of his cruising on that coast and told to keep to sea at all times possible.⁶⁵ Captain Newman (also spelled Newnham) of the sloop *Spy* was ordered to join the *Loo* and cruise with her until further orders.⁶⁶

The execution of Utting's plans was to be delayed, however, for the next day an "exstream hard gale of wind at ENE" struck the *Loo* as she lay at anchor off Charlestown Bar, obliging Utting to cut his "best bower cable"⁶⁷ and go to sea "for fear of a hurricane." For four days the *Loo* rode out the gale at sea, and when the storm was over Utting returned to his anchorage off Charleston, recovered his anchor and the next day (Saturday, October 25) "saild for Port Royall to refitt having received great damage in . . . masts and rigging."⁶⁸ Upon examining the damage to the *Loo*, Utting and his officers found the main yard sprung in three places and unserviceable. "The mainmast sprung in ye lower partners⁶⁹ about 6 inches in tho not to bad but shall be able to fish⁷⁰ him and make as serviceable as ever . . ." ⁷¹ Utting was mistaken, however, in his estimate of the damage, for closer examination revealed extensive damage to the mast

⁶¹ Ibid.

⁶² Ibid.

⁶³ ADM I, vol. 60, No. 436.

⁶⁴ Ibid.

⁶⁵ Ibid.

⁶⁶ Ibid.

⁶⁷ The cable of the heaviest of the two anchors carried in the bow of a ship. The bower anchors were those used for anchoring under ordinary conditions of wind and sea.

⁶⁸ ADM I, vol. 2625, No. 438.

⁶⁹ Planks fitted snugly around the base of a mast, a hatch, or a capstan covering the opening in the decks.

⁷⁰ To splice a broken spar or mast by binding with splints and wedging firmly.

⁷¹ ADM I, vol. 2625, No. 438.

below decks and the *Loo* was not to leave Port Royal until December 30, when she began her last cruise.

While lying at Port Royal Utting continued active direction of the vessels under his command from the *Loo*. On November 18 he issued two orders to Captain Newman of the sloop *Spy*. The first directed Newman to watch for a vessel expected from Havana with prisoners of war which were being exchanged and, should he meet with her, "to take out thirty of the best seamen on board for the service of his Majesty's ship *Loo*."⁷²

The second order directed the captain of the *Spy* to keep close touch with Charleston to obtain intelligence of the expected declaration of war against France, and if hearing of such declaration to rendezvous with the *Loo*.⁷³

By Captain Ashby Utting, Commander
of his Majesty's Ship *Loo*

Whereas we are in dayly expectations to hear of the Declaration of a French War.

You are hereby required and directed when on your cruise to call as often of Charles Town, as you shall think convenient to get the best information you can. And when you find any certain intelligence of a French War being declared either by Publick or private letters. You are immediately to proceed and joyn me of the N W part of the Grand Bahama, and if not find me there to proceed of the Isaack Rocks and the Bominies and if not at either of those places to proceed of Cape Florida and the Martiars [Fla Keys]⁷⁴ where you are to cruise for me Ten days and if not find me in that time you are to proceed to Hinds Bluff one of the Burry Islands where you are to fill up your water and then proceed and cruise between the N W part of the Grand Bahamas and Cape Florida till you meet me or as long as your provisions will last; and then return to Port Royall where you are to compleat your water and provisions to three months and to proceed to sea, and cruise between that Port and Georgia till further orders. Given under my hand on board the said ship in Port Royall Harbour the 18th day of November 1743.

Ashby Utting

To Captain Newnham of his
Majesties Sloop *Spy*.

⁷² ADM 1, vol. 2625, No. 426.

⁷³ ADM 2, vol. 2625, No. 426.

⁷⁴ Ponce de Leon named the Florida Keys "the Martyrs" because, he said, from the sea they bore a resemblance to the early Christian martyrs tied up on lines of stakes for execution. From 3 miles or so at sea the larger trees on the Keys indeed appear in long rows, the low-lying land of the Keys being out of sight over the horizon. In an age of Christian fervor, when religious significance was seen in every natural phenomenon, such an analogy would be the expected thing. The name "Martyrs" appeared on charts as late as the early 1800's.

On November 25 Captain Hamer of the *Flamborough* was also ordered to be on the lookout for the prisoner exchange ship expected from Havana, and to remove seamen for the *Loo*.⁷⁵

As work proceeded on repairing the storm damage to the rigging of the *Loo*, the carpenter discovered that the mainmast had been sprung in several places and reported to the Captain. Utting, on November 27, appointed the first and second lieutenants, the master,⁷⁶ the carpenter and the carpenter's mate to "take a strict and careful survey" of the mast and report its "exact condition" to him.⁷⁷ The survey board acted immediately and reported the same day that the mast had been severely sprung below decks and in their opinion was unfit for service.⁷⁸

For over a month the crew and officers turned to getting a mainmast cut and rigged, during which operations Warren Bolitha, the First Lieutenant of the *Loo*, broke three ribs, and on December 29, the day before the *Loo* sailed, he requested the captain to "let him go home in order to get cured."⁷⁹

While Utting was struggling to refit the *Loo's* damaged rigging, a letter arrived on December 14 from Capt. Charles Hardy of the *Rye* announcing that she, too, had sprung her mainmast. Utting immediately ordered Hardy to replace the mast "as soon as possible" and to return to his station off the Carolina coast. As a precaution against confusion on the part of the commanding officer of any ship that might relieve the *Rye* while the *Loo* was away on its expected cruise toward Cuba, Utting instructed Hardy to pass on his orders to his relief.⁸⁰

Meanwhile the *Flamborough* had been at sea and had fallen in with the ship that was bringing freed prisoners exchanged in Havana.⁸¹ On December 15 Utting ordered Captain Hamer to search out the *Spy*, which was then cruising off Charlestown Bar, and transfer to her, for transportation to the *Loo* at Port Royal, 30 of the seamen whom he had impressed, and then to proceed to cruise off Georgia, sending a boat to the Governor of that colony "for any intelligence he may have of any of the enemy's ships, or vessells being on that coast."⁸²

⁷⁵ ADM 1, vol. 2625, No. 432.

⁷⁶ Warships of this period had an officer in charge of the active sailing of the ship known as the Master.

⁷⁷ ADM 1, vol. 2625, No. 433.

⁷⁸ Ibid.

⁷⁹ ADM 1, vol. 2625, No. 431.

⁸⁰ ADM 1, vol. 2625, No. 430.

⁸¹ Among them, John Manley and Henry Spencer, who were to play a fateful part in the subsequent events. (ADM 1, vol. 2625, No. 446.)

⁸² ADM 1, vol. 2625, No. 434.

At the same time he ordered the *Spy* to take aboard the 30 seamen from the *Flamborough* and then to cruise off Port Royal Bar and join the *Loo* when she came out.⁸³

On December 22, Utting ordered Captain Ward of the ship *Tartar*, which had arrived to relieve the *Rye*,⁸⁴ to cruise on the Carolina and Georgia coasts on the *Rye's* old station.⁸⁵

Finally, on December 30, work on the *Loo* having been completed and the winds and tide favorable, the ship crossed the bar at Port Royal and began her last cruise. In a final letter to the Admiralty before the ship weighed anchor, Utting explained the long delay occasioned by damage the *Loo* had received in the storm off Charleston October 16-20, which he had underestimated in his letter to the Admiralty dated November 12, 1743, at Port Royal Harbor. He reported that it had taken him more than a month to get a new mast cut, partially seasoned, and rigged⁸⁶ and took occasion to point out again to the Lords of the Admiralty the desirability of cutting several trees and seasoning them as a reserve to be used for the manufacture of masts or yards in the event of further damage to the ships under his command.

At the same time Utting reported that he had relieved his first lieutenant, Mr. Bolitha, because of his injury, so that he could return home to England, and had promoted his second lieutenant and third lieutenant each one grade, then filling the vacancy left by the third lieutenant by the appointment of one William Lloyd whom he described as "a young gentm. well qualified for Preferment in his Maj's. service."⁸⁷

After this last word from Utting, the *Loo* sailed to her station in the Florida Straits and began cruising against Spanish shipping.

The morning of Saturday, February 4, 1744, found her cruising in the Straits off Havana. Around 8 o'clock in the morning a sail was sighted, and the *Loo* gave chase. As the stranger was neared, two seamen of the *Loo*, John Manley and Henry Spencer, who had been in the group of prisoners exchanged from Havana, informed Utting that they recognized the ship as the *Billander Betty* on which they had served. They told Captain Utting that while on a voyage in the

⁸³ ADM 1, vol. 2625, No. 427.

⁸⁴ Captain Newman of the *Rye* had been directed to convoy merchant ships to England from Charlestown in an order dated September 23, which was sent out by the *Tartar*. (ADM 2, vol. 60, p. 270.)

⁸⁵ ADM 1, vol. 2625, No. 429.

⁸⁶ ADM 1, vol. 2625, No. 424.

⁸⁷ ADM 1, vol. 2625, No. 424.

Betty (Capt. John Eades) from England to the Isle of May⁸⁸ and South Carolina they had been captured by a Spanish vessel off the coast of South Carolina. The Spanish put aboard a prize crew and sent the *Betty* on to Havana, but the Spanish vessel herself was lost in returning to Havana. While prisoners in Havana, Manley and Spencer had heard that the *Betty* had been converted to a "snow" and was to make a voyage to Campeche. About noon, when the *Loo* came alongside her chase, Utting sent an officer to examine the stranger's papers. Upon hearing that the master of the quarry could show only a common receipt, Utting decided to seize the ship for the proprietors of South Carolina and send her to Charleston.

Before sending her off, however, Utting requested that an "Irish gentleman" on the snow be brought aboard the *Loo* for questioning. Before this gentleman left the snow, he was seen to throw a large oil-skin packet overboard. A boat from the *Loo* retrieved the packet and Utting discovered that it contained papers in French and Spanish. At this, he decided to take the prize in, with the *Loo* as escort.

The examination of the prize had taken the entire afternoon, and when the *Loo* set sail with her charge it was 6 p.m. and growing dark. The "Pan of Matanzas" (fig. 1), a flat-topped mountain behind Matanzas Bay on the coast of Cuba, bore south by east at a distance of 18 to 21 miles.⁸⁹ Taking his fix on the mountain, Utting set sail and ordered a course northeast by north, the wind coming from the southeast. This course was kept until midnight, when Utting, believing that he was clear of the Double Headed Shot Key in the western end of the Salt Key Bank, instructed Randell, the first lieutenant and officer of the off-going watch, to alter the course to northeast and went below to his cabin to rest, having been continuously on deck since early morning.⁹⁰

Shortly after, Randell was relieved of the watch by Robert Bishop, the master. Randell relayed these instructions to Bishop, reminding him to have the deep-sea lead line cast every half hour,⁹¹ and went

⁸⁸ "Maio" in the Cape Verde group occupied until the end of the eighteenth century by the English, who claimed a right to the island under the marriage treaty between Charles II and Catherine of Braganza of Portugal. The English occupation is recalled in the name "English Road," which the port of Nossa Senhora de Luz is sometimes called.

⁸⁹ The bearing and the distance to the Pan of Matanzas were given by Lt. James Randell in his deposition to the court martial that tried Captain Utting. (ADM 1, vol. 5283.)

⁹⁰ Utting's letter of February 15, 1744. (ADM 1, vol. 2625. (See Appendix B.))

⁹¹ Bishop's deposition at the court martial. (ADM 1, vol. 5283.)

below. Nothing to arouse the suspicion of Utting or Randell had been seen during the latter's watch. The night was dark and cloudy, with visibility not over a quarter of a mile.⁹²

At 12:30 a.m. and again at 1:00 the deep-sea lead line was cast according to orders, and no bottom was found at 300 feet. At about 1:15 Bishop sent the lead-line crew to the side to clear the line for heaving and followed them to the gunwhale himself to see to this. To his great surprise he found the ship in "white water" and saw breakers ahead. He instantly "ordered the helm alee" and sent a message down to Captain Utting⁹³ to call him on deck. As Utting rushed on deck he found the ship coming about into the wind and away from the reef on which the breakers were rolling. As the ship veered off the wind the head sails were caught across wind and the ship struck the reef



FIG. 1.—The Pan of Matanzas from a vignette appearing on an English chart dated 1794.

aft.⁹⁴ At this the mainsail was set "in order to press her off," and Utting ordered a boat out to sound around the ship.⁹⁵ The officers and men off watch and sleeping below were awakened by the shock of the ship striking the reef. John Vivian, the carpenter, rushed aft, whence the shock had come, and found the tiller broken off. He reported this to Utting just as another swell caught the ship and broke off the rudder, at which she began shipping water in the hold. Utting ordered all pumps manned, and the water in the hold began to fall, but as the crew was getting out the boats "three or four severe seas" crushed the ship against the reef and she began sinking rapidly.⁹⁶

When it became apparent that the ship could not be saved, Captain Utting ordered Mr. Bishop and Gunner Samuel Kirk to save as much

⁹² Deposition of John Randolph, master's mate, at the court martial of Captain Utting. (ADM 1, vol. 5283.)

⁹³ Bishop's deposition. (ADM 1, vol. 5283.)

⁹⁴ Utting's letter of February 15, 1744.

⁹⁵ Bishop's deposition. (ADM 1, vol. 5283.)

⁹⁶ Utting's letter of February 15, 1744.

of the bread and gunpowder as possible before the water rising in the hold ruined it. Bishop was able to save 20 bags of bread before the water forced him from the breadroom, and by the efforts of Gunner Kirk 6 barrels of gunpowder were saved.

The prize, which had struck the reef just after the *Loo*, was rolling and pounding herself to pieces on the coast and, in order to save the men aboard her, Utting ordered her masts cut away and her guns and

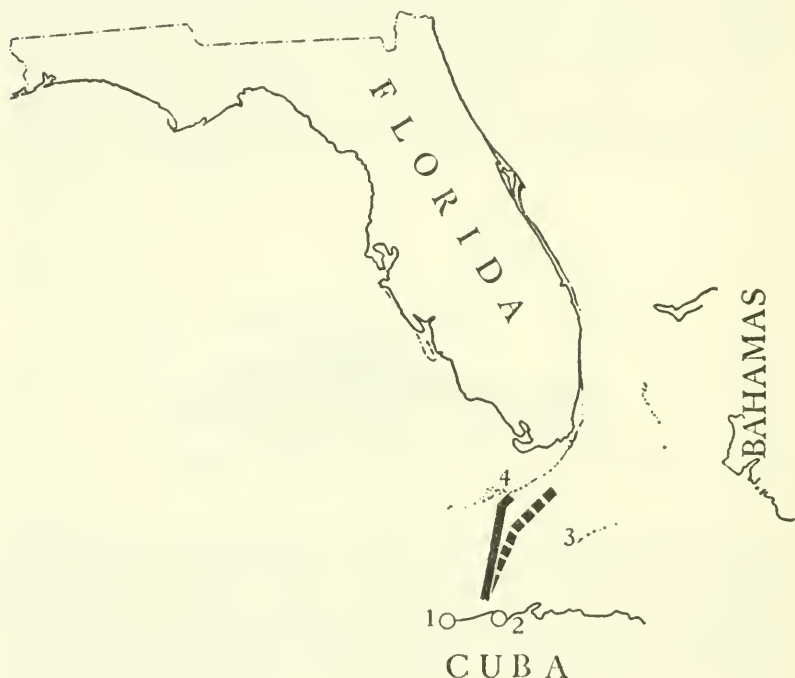


FIG. 2.—Map of the Florida Straits, showing the course of the last cruise of the *Loo*. 1, Havana. 2, Pan of Matanzas. 3, Double Headed Shot Key. Dotted line, Captain Utting's intended course. Solid line, actual course of the *Loo*.

anchors thrown overboard. After this she lay more quietly in the swell and her men were saved.

With the coming of daylight Utting and his officers saw with great surprise that they were ashore on a "small sandy Key about $1\frac{1}{2}$ cables⁹⁷ length long and $\frac{1}{2}$ broad which lay on the edge of the Bank of the Martiers 3 leagues⁹⁸ without them."⁹⁹ (See fig. 2.)

At no time since the ship had struck had the pilots or officers

⁹⁷ A cable was 600 feet.

⁹⁸ A league was 3 nautical miles.

⁹⁹ Utting's letter of February 15, 1744.

doubted that they were aground on Double Head Shot since, under normal circumstances, the course that they had steered could not have carried them to the Florida Keys. Utting sent Lieutenant Randell ashore to see if fresh water was to be had there, but he found none.¹⁰⁰ As full daylight came Utting landed all the men from the *Loo* and the prize with the exception of a few who were employed in cutting holes in the frigate's deck to recover casks of water and such other supplies as could be saved. At about 10 o'clock, to Utting's great joy, a sloop was sighted offshore and a signal was made to her, but the sloop stood out to the northwestward.¹⁰¹ The captain immediately armed all the boats and with Lieutenant Randell and Mr. Bishop in command sent them in pursuit, instructing them to exert every effort to bring the sloop in, since it probably would be their only chance of succor.

The desperate situation of the group was evident to all. Here were some 280 men stranded on a small sandy islet just off a hostile coast swarming with the savage Caloosa Indians who murdered Englishmen on sight.¹⁰²

To add to the insecurity was the evident fact that in a blow of any force the whole islet would be swept by waves.

At night Utting posted watches, each consisting of 25 marines and 25 sailors, around the island at the water's edge as "centenells" to prevent a surprise night attack from the Caloosas "the Indians having numbers of canoes."¹⁰³

The next morning (Monday) as daylight came, Utting and the men ashore were overjoyed to see the boats bringing in the sloop. As they came ashore Randell and Bishop reported that on the approach of the armed boats the Spanish crew had abandoned the sloop and were no doubt now headed for Havana in their boat.

Meanwhile the men, frightened and confused, became "very rebellious and mutinous dividing into parties and growling amongst themselves,"¹⁰⁴ claiming that the officers no longer had authority over them, and clamored to leave the island immediately. Utting took no notice of them but, with the men who would work, continued efforts to recover water and other provisions from the wreck.

All day Tuesday was spent in getting water casks from the *Loo's* hold and in getting the sloop and boats ready for the escape. The

¹⁰⁰ Randell's deposition.

¹⁰¹ Ibid.

¹⁰² Spaniards fared a little better, as the Caloosas knew they could be ransomed.

¹⁰³ Utting's letter of February 15, 1744.

¹⁰⁴ Ibid.

capacity and safety of the longboat were increased by adding planks to the gunwhales, giving her a higher freeboard and decreasing the chances of shipping water in a seaway while heavily loaded. Thus altered, the boat was able to carry 60 men.¹⁰⁵

At about noon the next day, Wednesday, February 8, all the men were embarked—60 in the altered longboat, 10 in the yawl,¹⁰⁶ 184 “in the little Sloop not 30 tuns”¹⁰⁷ and 20 in the captain’s barge. Utting sent the sloop, the longboat, and the yawl 3 or 4 miles offshore while he remained behind with the men detailed to the barge and laid most of the gunpowder which had been saved and some other fuel along the starboard gun deck of the *Loo*, the only deck remaining above water. By 2 o’clock all the preparations were completed and Utting fired the ship. As they rowed away the ship blazed to the top of her masts and blew up “in several places and was in flames fore and aft.”¹⁰⁸ The burning ship was visible until sunset and while her hull was completely destroyed, Utting feared that the Spaniards would return and salvage her guns and anchors, since intelligence of the *Loo*’s end would be communicated to the Spanish in Havana by the escaped crew of the sloop.

Utting’s plight was still grave, since the sloop was very much overloaded and would have capsized in a blow. He placed First Lieutenant Randell and Third Lieutenant Lloyd in charge of the longboat, his Sailing Master Bishop was given command of the barge and “a mate” assigned to the yawl. Utting remained in command of the sloop. The motley fleet set a course for the Bahamas, the boats being ordered “in case of separation to make the best of their way over to the Bahama Bank for Providence.”¹⁰⁹

That night Utting carried a light to guide the boats, but they out-sailed the overloaded sloop and at midnight were lost from sight when Utting had to tack and stand to the northward after signaling his change of course with the light. At daybreak the boats were gone, and Utting, feeling that they were bound for Providence and being unable to set sail for an easterly course, set a course for South Carolina. In his report to the Admiralty he summed up the desperate situation in which he found himself with the overloaded sloop: “it blowing fresh and the sloop top heavy with men could not carry sail so obliged to

¹⁰⁵ Ibid.

¹⁰⁶ A heavy double-ended rowboat.

¹⁰⁷ Utting’s letter of February 15, 1744.

¹⁰⁸ Ibid.

¹⁰⁹ Ibid. Providence had been settled in the seventeenth century.

bear away and take my fate through the Gulph of Florida ¹¹⁰ for any port of Carolina even for St. Augustine (if I could fetch nowhere else) rather than all be drowned which Doe assure you had very little other prospect." ¹¹¹

The fair weather continued and the overloaded sloop arrived in Port Royal harbor (pl. 17) on the night of February 13. Utting and the men were worn out from physical and mental strain, all realizing that their escape from capture or drowning was just short of miraculous.

Upon his arrival at Port Royal Utting began immediate steps to assemble evidence to protect himself in the court martial that he had to face for the loss of the *Loo*. His first step was to send one of his pilots, William Lyford, to the town of Beaufort 6 miles north of Port Royal to give a deposition before Robert Thorpe, justice of the peace. In the deposition Lyford stated that in his opinion the course the *Loo* had steered before she ran aground "was the best through the Gulph (and is generally allowed so to be) and was then of the opinion that such course would carry the said ship nearer the Bahama shore than the Florida; and this deponent further deposith and makes oath, that he is well acquainted with the Gulph of Florida having used it these thirty years past." ¹¹²

Eight days later, on February 21, Utting was in Charleston starting proceedings to prove that the prize which he had taken was a legal one. John Manley and Henry Spencer, the two seamen who had recognized the prize as their former ship, appeared before James Grome, judge of the Court of Vice Admiralty of the Province of South Carolina, and swore under oath that the prize was the former *Billander Betty*, and that while on a voyage from England to the Isle of May and South Carolina, it had been captured off the coast of South Carolina on April 9, 1743—

by a Spanish vessell bound from the Havannah to St. Augustine with about sixty or more soldiers on board, that the said vessell not being able to make St. Augustine return'd to the Havannah and in her passage was cast away, that the *Billander* so taken as aforesaid was carried to the Havannah and was there converted into a *Snow* and intended on a voyage to Campeachee but afterwards these Deponents hear'd that she was bound for the Mississippi.

That these Deponents came to this province with the Flag of France and were press'd on Board his Majestys Ship the *Loo* under the command of Capt. Ashby Utting, that on a cruise in the said ship they met with a *Snow* which these Deponents very well knew to be the *Billander Betty* taken as aforesaid

¹¹⁰ The Gulf Stream would carry him northward.

¹¹¹ Utting's letter of February 15, 1744.

¹¹² Deposition accompanying Captain Utting's letter of February 15, 1744.

by the Spaniards and converted into a Snow that the said Snow was taken by the Loo about a fourthnight ago, viz the 5th of this instant February and cast away with the said Man of War about nine leagues to the westward of Cape Florida.¹¹³

On March 6, as the hearing proceeded, this deposition was introduced to the Court of Vice Admiralty as "Exhibit Marked I" and undoubtedly had a great influence in the outcome of the case in Utting's favor.

By March 12 the proceedings in the Vice Admiralty Court seem to have been concluded. Utting had only to wait for the return of his officers from the Bahamas, and then a warship for transportation to England if his court martial could not be held in America.¹¹⁴

The loss of the *Loo* had immediate repercussions in the colony of South Carolina, and on the same day the case in court was concluded, the Governor, James Glen, wrote a lengthy letter to the Lords of Trade in which he indicated the fears of invasion which had swept the southern frontier of the colony:

After writing so lately by Captain Hardy,¹¹⁵ I had not so soon troubled your Lordships with another letter, but the loss of his Majestys Ship the Loo makes it my duty; this unlucky accident happened the fifth of February about one in the Morning, by her running on some rocks called the Martyres to the South West of Cape Florida.

... my principal concern is to express to your Lordships how sensibly that loss affects this province. The long neglected Town of Beauford, upon the arrival of this Ship, and the assurances given that another would be sent out, began to revive, and many good houses were built, and many grants for Town Lotts were applyed for, so that I am persuaded that Town and the adjacent Country, would soon have been well settled, and consequently our Southern Frontier, where we are most vulnerable, would have been strengthened, but now I receive letters and petitions dayly from the best People in those parts, representing their fears and the dangers to which they are exposed, and everything is at a stand, tho' I have stationed one of our gallys (a very fine small vessel) there, I have likewise desired the Captains of the Man of War on this station, to keep a particular eye upon that Port, in their Cruizes along our coast.¹¹⁶

¹¹³ Copies of papers relating to the proceedings of the Court of Vice Admiralty sent by Captain Utting to Thomas Corbett after his return to England (ADM 1, vol. 2625, No. 455.)

¹¹⁴ Utting and his wife had been residents of South Carolina several years. The wait for transportation to England was probably not too burdensome to Utting.

¹¹⁵ Of the *Rye*, which had sailed for England a short time before Utting reached Port Royal.

¹¹⁶ Letter of James Glen dated March 12, 1743/44. Colonial Office original correspondence, CO5, vol. 370, pp. 141-142, Public Record Office, London.

He then went on to point out the suitability of Port Royal as a harbor and its strategic location in relation to the Florida Straits and the Spanish trade routes:

And as most of the trade and treasure of France and Spain must come through the Gulf of Florida, where can it be so properly waited for as here, where a few great ships stationed, to cruize betwixt this and Cape Florida, a very easy navigation, must become masters of everything.¹¹⁷

The Governor reported that Captain Dansant, captain of the *Loo's* prize, would be sent off without being permitted to see the fortifications of Charleston, and "The forty-four marines belonging to the *Loo*," he stated, were being "lodged at the expense of this government and shall be well taken care of."¹¹⁸ The sailors were no doubt taken into the other ships present on the station, the Governor not mentioning them.

Governor Glen spoke a good word for Captain Utting with the Lords of Trade, describing him as "a Gentleman who by a long residence in this Province, has established a character amongst all ranks of people here, for strict honors and veracity, as well as for his care, diligence, and knowledge, as an officer."¹¹⁹

Early in April Utting and his officers, who had arrived from the Bahamas, sailed for England and arrived there late on the night of May 24. The next day Utting reported his arrival to the Admiralty and requested an early court martial for the loss of the *Loo*. (See fig. 3.)

Six days later, May 31, the court of 12 captains sat on board the ship-of-the-line *Sandwich* with Vice Admiral James Steuart presiding. After a consideration of the depositions and testimony of Utting and his officers the Court was "unanimously of the opinion that Capⁿ. Utting and his several officers did in no wise contribute to her going ashore, but that it was owing to some unknown accident, it appearing to the Court, that the course the ship steered was a good one, and must have carried her thro the Gulph of Florida, with all safety had not some unusual current rendered the said course ineffectual."¹²⁰

On June 6 the Lords of the Admiralty ordered the Navy Board to procure funds from the Treasury and pay the officers and men of the *Loo* through the day she was lost. On August 10, 1744, the officers and men gathered on Broad Street in London and were paid the 1,510

¹¹⁷ Ibid.

¹¹⁸ Ibid.

¹¹⁹ Ibid.

¹²⁰ Report of Court Martial dated June 1, 1744, Admiralty In-Letters, ADM 1, vol. 5283.

Sir

Please to Acquaint their Lordships
that I arriv'd here late last night, from So
Carolina; wth my two Heads Master, Gunner
Boatswain, Carpenter, Purser, & one of the
Mates, y^e Second Lieut. & y^e Other-mates, being
arriv'd about a Month since; the Ships
Company, & Petty Officers, are distributed
amongst y^e most Ship^{ps}, w^{ch} are bound for
Eng^l. Except about 20 w^{ch} are on board
the men a war their y^e Manners wth their
Officers lost at Carolina: y^e Officer being of the
Opinion he could not proceed, wthout further
Orders from his Gov^t. I should have come
from Carolina sooner, but as my ^{Officers} w^{ch} were
at Providence, was not come to Carolina
I thought it my Duty to stay to collect
them together & bring them home wth me.
Which I hope their Lordships will approve

I also beg you'll please to move their Lord-
ships, for an Order, for a Court martial for
the Loss of his Maj^{ty} Ship *Loo*. w^{ch} is
under my Command.

May 21. 1744

Yours
Sir

W^{ch}

The Hon^{ble} The Lords & C^o of the Admiralty
Ashby Utting

Fig. 3.—Letter of Capt. Ashby Utting to the Secretary of the Admiralty reporting his arrival in England May 24, 1744, to stand trial by court martial for the loss of the *Loo*. (Photostat from the Public Record Office, London.)

pounds 4 shillings 11 pence due them after deductions of 1,121 pounds 4 shillings 11 pence for tobacco, clothing, hospital fund, pay advances, etc. James Compton, Captain, Royal Navy, a Navy Commissioner, kept an eye on the proceedings while navy clerks Stephen Mercer and Philip Stephens and treasury clerks John Wilson and Thomas Vaughn checked the pay list and disbursed the money.¹²¹

After his acquittal Utting attended the Secretary of the Admiralty frequently while waiting for an answer to his request for another command. On June 12 he discussed with the secretary the possibility of getting command of the *Mary Galley* and the next day advised Corbett that several of the men and petty officers of the *Loo* desired to ship with him on his next cruise. He also reminded Corbett of the desirability of his return to the Carolina station since his wife was there.¹²²

On July 7, 1744, a commission was issued giving Utting command of the *Gosport*.¹²³ While fitting out his new ship, Utting continued to hope that he would be able to get orders to return to the Carolinas. No one knew better than he the danger of invasion to which the colony was exposed through the loss of the *Loo*, and he was anxious for the safety of Mrs. Utting, who was at Port Royal. His fears were multiplied when, on August 10, he received a letter from his wife, dated July 5, in which she reported that the settlements south of Charleston had been evacuated because of fear of an invasion and that she was a refugee in the provincial capital. Utting's patience reached the breaking point as he pleaded for orders to America: "This is a very shocking affair both to her and me and beg for God's sake you'll be so good to use your interest with Lord Winchelsea ¹²⁴ to git me to some part of America." ¹²⁵

The exigencies of war, however, outweighed the personal problems of Utting, and he was ordered to the Baltic to convoy a fleet of merchantmen to Elsinore, Denmark, and Bergen, Norway.

On October 13 Utting was back in England with the convoy from Bergen. The next month he took a convoy to Ostend, leaving on the 15th and returning to England on the 24th, assuming command of the *Aldborough* sometime between his return and November 29 under a commission dated November 7.¹²⁶ Utting's wish to return to South

¹²¹ *Loo's* pay list dated Aug. 10, 1744, Admiralty Ships Pay Books, Treasurers Series I, ADM 33, No. 352.

¹²² Admiralty In-Letters, ADM 1, vol. 2267.

¹²³ AD 6/16, Commission and Warrant Book, 1743-1745, p. 335.

¹²⁴ First Lord of the Admiralty.

¹²⁵ ADM 1, vol. 2625, No. 477.

¹²⁶ AD 6/16, Commission and Warrant Book, 1743-1745, p. 380.

Carolina was realized shortly after, when he was ordered to escort a convoy to America and assume his former command as senior officer present at Charleston. On March 26, 1745, he arrived at his old station and began the direction of naval operations off the Carolinas. The threat from the Spanish was still real, and naval patrols were necessary to prevent surprise attacks on the coastal settlements.

Sickness plagued the *Alborough* and Utting was unable to keep the sea as he should have. Enemy privateers arrived off the coasts of Carolina and Georgia, and the captain was at his wit's end to protect the coastal settlements from Fredrica, in Georgia, to Charleston with his little squadron. As a result some discontented merchants in Charleston complained to the Carolina proprietors that Utting was not doing his duty. These complaints seem to have been unjustified, for the Governor, Council, and several principal merchants refused to sign them. Thus misfortune harassed Utting during his last cruise until early in January 1746, when he died on board the *Alborough* in Rebellion Road, Charleston, just after returning from a patrol off the coast.

On April 18, 1744, while Utting was on the high seas returning to face a court martial for the loss of the *Loo*, the Lords of the Admiralty had ordered the Navy Board to "cause a new ship of forty-four guns to be built in the room of the Looe lately lost near the Gulph of Florida."¹²⁷ Today the name "Looe" is perpetuated by the submerged reef lying off the central Florida Keys, visited by occasional fishermen who must wonder at the strange name it bears, never dreaming that the quiet little reef was once the scene of as dramatic a story of shipwreck and rescue as can be found in the annals of the English colonies in America.

¹²⁷ Admiralty Out-Letters, ADM 2, vol. 205, p. 344.

APPENDIX A

EXTRACTS FROM THE NAVY LIST RELATING TO THE "LOO"

<i>Period</i>	<i>Duty</i>
April 1, 1707–May 31, 1707	"Longreach taking in Guns"
June 1, 1707–June 30, 1707	"Going to Archangell"
July 1, 1707–September 30, 1707	"Gon to Archangell"
October 1, 1707–October 31, 1707	"Arch-Angell"
November 1, 1707–November 30, 1707	"Returned with the Russia ships to Grimsby"
December 1, 1707–January 31, 1708	"Sheerness (fitting for Newfoundland)"
February 1, 1708–March 31, 1708	"Downes for Newfoundland"
April 1, 1708–April 30, 1708	"for Newfoundland"
May 1, 1708–July 31, 1708	"Gon to Newfoundland"
August 1, 1708–February 28, 1709	"at Newfoundland"
March 1, 1709–July 31, 1709	"coming convoy from Newfoundland"
August 1, 1709–September 30, 1709	"Coming convoy from Lisbon but last from Newfoundland"
October 1, 1709–October 31, 1709	"Sheerness—refitting"
November 1, 1709–November 30, 1709	"Sailed to Join the Tilbury Etc. at Goree and when she returns to join the Gosport and Strombolo between Dover and Beachy"
December 1, 1709–December 31, 1709	"Downes ordered to cruise between Dover and Beachy head" ¹
January 1, 1710–January 31, 1710	". . . Dover and Beachy head"
February 1, 1710–February 30, 1710	"Cruizing between Dover and Beachy head"
March 1, 1710–March 31, 1710	"Holland—ordered to cruise between Dover and Beachy Head"
April 1, 1710–April 30, 1710	"Holland, to come to the Downs"
May 1, 1710–May 31, 1710	"Dunkirke Squadron" "Sailed to Cruise on ye French Coast between Cape Barfleur and Harve de Grace"
June 1, 1710–June 30, 1710	"Dunkirke Squadron" "Margate Roads ord. to Holland with the yachts and bring the Queen's wine to the Nore"
July 1, 1710–July 31, 1710	"Dunkirke Squadron" "Holland ord. to bring the Queen's wine to the Nore"
August 1, 1710–September 30, 1710	"Gone Convoy to the East Country"
October 1, 1712–October 31, 1712	"At the Nore"
November 1, 1710–December 31, 1710	"Sheerness Refitting"
January 1, 1711–January 31, 1711	"Downes ordered to Scarboro to bring a ship to the Nore"

¹ Navy List, January 1, 1707–December 31, 1709, ADM 8/10.

<i>Period</i>	<i>Duty</i>
February 1, 1711–February 28, 1711	"Spithead, ordered to the Downes"
March 1, 1711–March 31, 1711	"In Holland to return to the Downes"
April 1, 1711–April 30, 1711	"In Holland to bring the Queen's wine to the Nore"
May 1, 1711–May 31, 1711	"Sheerness, ordered to the Downes"
June 1, 1711–June 30, 1711	"Ously Bay, for Russia"
July 1, 1711–September 30, 1711	"Gone Convoy to Russia"
October 1, 1711–October 31, 1711	"Coming from Russia, the 1st Convoy"
November 1, 1711–November 30, 1711	"at the Nore"
December 1, 1711–December 31, 1711	"Sheerness refitting" ²
January 1, 1712–March 4, 1712	(No record found)
March 5, 1712–June 30, 1712	"Convoy between Folmouth and Spithead"
July 1, 1712–July 31, 1712	"Cruizing for the homeward bound Virginia ships"
August 1, 1712–September 30, 1712	"Cruising off the Orcades for the homeward bound Virginia ships"
October 1, 1712–October 31, 1712	"Nore, ordered to the Downes"
November 1, 1712–November 30, 1712	"Downs, ordered to Bayonne with the Transports"
December 1, 1712–December 31, 1712	"Gone to Bayonne with transports for soldiers"
January 1, 1713–January 31, 1713	"Gone to Bayonne for some prisoners of war"
February 1, 1713–February 28, 1713	"Coming from Kinsale to Plyo. to fit and repair to Spithead"
March 1, 1713–March 31, 1713	"Kinsale, ordered to Plymo. to fit and repair to Spithead"
April 1, 1713–May 31, 1713	"Plymouth refitting and ordered to Spithead"
June 1, 1713–June 30, 1713	"Spithead, ord. ^d to Guernsey and Jersey for some disbanded men of Mordaunts Regiment."
July 1, 1713–July 31, 1713	"Gone to Gurnsey and Jersey for some disbanded soldiers"
August 1, 1713–September 30, 1713	"Spithead cruizing between Start and the Isle of Wight"
October 1, 1713–October 31, 1713	"At Portsmouth to fit and cruiz between ye Start and the Isle of Wight"
November 1, 1713–December 31, 1713	"To intercept the traders cruizing between Start and the Isle of Wight" ³

² Ibid., January 1, 1710–December 31, 1711, ADM 8/11.

³ Ibid., March 5, 1712–December 31, 1713, ADM 8/12. Constant patrol of these waters was maintained in an effort to prevent the smuggling of wool from Britain to the Continent, the export of raw wool being absolutely forbidden at this time.

<i>Period</i>	<i>Duty</i>
January 1, 1714–March 31, 1714	"To intercept the traders cruising between the Start and the Isle of Wight"
April 1, 1714–April 30, 1714	"At Portsmouth fitting and then returns to her station"
May 1, 1714–June 30, 1714	"In the Downes going to Port Mahon with a storeship."
July 1, 1714–September 30, 1714	"Gone to Port Mahon with a storeship"
October 1, 1714–October 31, 1714	"Coming from Port Mahon"
November 1, 1714–December 31, 1714	"At Shearness refitting" ⁴
January 1, 1715–January 31, 1715	"ordered to be laid up and paid off"
February 1, 1715–March 14, 1717	(Not in service)
April 1, 1717–October 31, 1717	"Baltick Squadron"
	"Hosp. Ship Looe"
November 1, 1717–December 31, 1717	"To be paid off and laid up . . . Depford"
January 1, 1718–March 25, 1718	(Laid up)
March 26, 1718–March 31, 1719	"Hosp. Ship Looe"
	"Mediterranean Squadron"
April 1, 1719–April 30, 1719	"Looe . . . 125 men 30 guns" (refitted as warship?) "Mediterranean Squadron"
May 1, 1719–December 31, 1720	"Mediterranean Squadron"
January 1, 1721–April 30, 1721	"Port Mahon" ⁵
May 1, 1721–January 31, 1722	"In the Mediterranean"
February 1, 1722–May 31, 1722	"Ordered home from Mediterranean"
June 1, 1722–August 31, 1722	(Lists missing)
September 1, 1722–December 31, 1725	(Not in lists, laid up) ⁶
January 1, 1726–January 10, 1728	(Laid up)
January 11, 1728–March 31, 1728	"At Woolwich"
April 1, 1728–April 30, 1728	"At Longreach"
May 1, 1728–July 31, 1728	"Nore"
August 1, 1728–December 31, 1728	"Downes to examine ships" ⁷
January 1, 1729–January 31, 1729	"Woolwich, not sheathed"
February 1, 1729–April 1, 1729	(Laid up)
April 2, 1729–May 31, 1729	"Woolwich fitting for Channel Service"
June 1, 1729–July 31, 1729	"Downes"
August 1, 1729–August 31, 1729	"Downes—Channel"
September 1, 1729–September 30, 1729	"At Diep ordered to Spithead"
October 1, 1729–December 31, 1729	"At Spithead"
January 1, 1730–March 31, 1730	"Portsmouth Harbour"
April 1, 1730–April 30, 1730	"Portsmouth Harbour, refitting for Channel service"

⁴ Ibid., January 1, 1714–December 1, 1714, ADM 8/13.

⁵ Ibid., January 1, 1715–April 30, 1721, ADM 8/14.

⁶ Ibid., May 1, 1721–December 31, 1725, ADM 8/15.

⁷ Ibid., January 1, 1726–December 31, 1728, ADM 8/16.

<i>Period</i>	<i>Duty</i>
May 1, 1730–May 31, 1730	"Spithead—Channel"
June 1, 1730–June 30, 1730	"Gone with the money and clerks to Plymouth"
July 1, 1730–July 31, 1730	"Ordered to fitt for Gibraltar, Spithead"
August 1, 1730–October 31, 1730	"Gone to Gibraltar as convoy to the transports"
November 1, 1730–January 31, 1731	"To remain in the Mediterranean"
February 1, 1731–May 31, 1731	"Cruizing on the Coast of Barbary"
June 1, 1731–July 31, 1731	"Cruizing on the Coast of Sallee"
August 1, 1731–August 31, 1731	"Ordered Home" "From the Coast of Sallee"
September 1, 1731–November 30, 1731	"Portsmouth refitting for Channel Service"
December 1, 1731–December 31, 1731	"Stationed between the Start and the Isle of Wight"
January 1, 1732–January 31, 1732	"Stationed between the Start and the Isle of Wight"
February 1, 1732–February 28, 1732	"Ordered to the Downes" ⁸
March 1, 1732–March 31, 1732	"Start and Isle of Wight"
April 1, 1732–April 30, 1732	"Portsmouth, ordered to Plymouth"
May 1, 1732–May 31, 1732	"At Spithead, Channel Service"
June 1, 1732–December 31, 1734	"Gone to Plymouth with money and clerks"
January 1, 1735–May 4, 1735	"Nore"
May 5, 1735–June 30, 1735	(Not listed, laid up) ⁹
July 1, 1735–July 31, 1735	(Not listed, laid up)
August 1, 1735–August 31, 1735	"Sheerness, fitting for the Channel"
September 1, 1735–October 31, 1735	(Again as a hospital ship)
November 1, 1735–April 30, 1737	"At the Nore"
May 1, 1737–May 31, 1737	"At Spithead"
June 1, 1737–December 31, 1739	"Gone to Lisbon with Sir John Norris"
January 1, 1740–December 31, 1741	"At Lisbon"
January 1, 1742–January 3, 1742	"To be paid off"
January 4, 1742–April 30, 1742	(Not listed, laid up) ¹⁰
May 1, 1742–May 31, 1742	(Not listed, laid up) ¹¹
June 1, 1742–June 30, 1742	(Laid up)
	"Loo, 44 guns . . . Earl of Northesk Commander, Depford fitting for Channel Service"
	"At the Nore to convoy transports from the Downes to Spithead"
	"At Portsmouth refitting for channel service"

⁸ Ibid., January 1, 1729–December 31, 1731, ADM 8/17.

⁹ Ibid., January 1, 1732–December 31, 1734, ADM 8/18.

¹⁰ Ibid., January 1, 1735–December 31, 1739, ADM 8/19 and 8/20.

¹¹ Ibid., January 1, 1740–December 31, 1741, ADM 8/21.

July 1, 1742–August 31, 1742	"Cruizing 50 leagues off Capte Finis- terre"
September 1, 1742–September 30, 1742	"Plymouth refitting for Channel Serv- ice"
October 1, 1742–October 31, 1742	"In St. George's Channel for 3 weeks"
November 1, 1742–November 30, 1742	"Plymouth"
December 1, 1742–December 31, 1742	"Spithead to clean at Portsmouth"
January 1, 1743–March 31, 1743	"Portsmouth to cruize from 30 to 50 lgs. W.S.W. of Cape Clear for 6 weeks"
April 1, 1743–April 30, 1743	"Plymouth, refitting for channel serv- ice"
May 1, 1743–May 31, 1743	"To cruize between Bibao and St. Jean de Luz, to intercept some Caracca ships expected at St. Sebastian . . . to cruize 6 weeks on the Station"
June 1, 1743–June 30, 1743	"Cruizing between Bilbao and St. Jean de Luz to intercept some Caracca ships expected at St. Sebastian . . ."
July 1, 1743–July 31, 1743	"Portsmouth refitting for North America"
August 1, 1743–August 31, 1743	"To attend on So. Carolina"
September 1, 1743–April 30, 1744	"South Carolina"
May 1, 1744–	(No entry. ¹² The <i>Loo</i> had been lost February 5, 1744. Word apparently did not reach the Admiralty clerk keeping the navy lists until sometime in April. Entries of the location of ships were made on the first day of the month.)

¹² Ibid., January 1, 1742–May 1, 1744, ADM 8/22, 8/23, and 8/24.

APPENDIX B

LETTER FROM CAPTAIN ASHBY UTTING TO THE ADMIRALTY REPORTING THE LOSS OF THE "LOO"

Port Royall

15th February, 1744.

I am extremely sorry this should be the messenger of such disagreeable news as the loss of H.M.S. Loo.

Will you please acquaint their Lordships that on the 4th day of February I was cruising on the station 8 leagues from the Cape of Florida when about 8 in the morning I saw a sail which I gave chase to and about noon spoke with her, she being an English "Snow"¹ from Havannah and Missippy, but sailed by Frenchmen and two Spaniards, one that had been lately taken from the English and carried into Havannah. I having two men on board which was taken in her and the master having no copy of the condemnation and nothing to show for the sale but a common receipt. I seized her for the proprietors and was designed to send her into Charlestown but at the same time an Irish gentleman, a merchant that I had sent for on board, heaved a large packet overboard, which my boat took up and when opened found it full of French and Spanish papers, I then determined to see her in myself and also took her in tow. By the time I made sail it was 6 in the evening at which time the Pan of Mattances² bore S b E, the wind being SE. I steered NE b N till 12 at night by which time I was well assured I was got to the northward of the double Head Shott,³ then hauled up NE. Till this time I was on deck myself and when thought I was passed all danger went and sat down in the cabin (as Doe assure you I did not go to bed one night in six of the time I was cruising here).

At a $\frac{1}{4}$ past one in the morning, the officer of the watch sent down to let me know he was in the middle of brakers and must Doe him the justice to say he behaved like an exceedingly good officer for before I was got upon deck which could not be ten moments, he had put the helm a Lee and the ship was at stays,⁴ just as we hauled the main top sail the ship struck abaft but she pay'd off so far as to haul the head sails,⁵ when the Captain⁶ came and told me the tiller

¹ A brig having a small trysail mast set astern of the mainmast. The trysail was a fore and aft sail with a gaff and, in some cases, a boom.

² A high, flat-topped hill lying inland from Matansas Bay on the northern coast of Cuba, a point on which mariners take bearings in setting a course up the Florida Straits (see fig. 1).

³ A group of keys lying in the eastern end of the Salt Key Bank which extends to the center of the southern end of the Florida Channel (New Bahama Channel).

⁴ A vessel is said to be "at stays" when heading into the wind in tacking.

⁵ Swung off from the wind so far that the head sails were caught across the wind pushing the bow of the ship around toward the reef.

⁶ The sailing master.

was broke short off the ship, continued striking, I ordered all the boats out as far as possible. Immediately after he came and told me the rudder was gone and that she made some water in the hold but not much, we set all the pumps to work as you must believe on this occasion, and rather gained on her. By this time we was getting the long boat out when there came three or four severe seas and bulged⁷ her immediately and had 5 foot water in the hold; I ordered the master and gunner to come and save what bread and powder they could before the water was over all, which they did and saved 20 bags of bread and 6 barrels of powder⁸ which was all we could save.

By this time the "Snow" which shared the same fate, was on her broad side, the ship striking much and taring all to pieces, and having no prospect of getting her off, ordered the masts to be cut away and all the upper deck guns and anchors to be thrown overboard, that she might lay quiet and by that means save the men which by good fortune she did, though all this time thought I was got on the double head Shott Bank when at daylight to my great surprise we was getting on a small sandy key about $1\frac{1}{2}$ cables⁹ length long and $\frac{1}{2}$ broad which lay on the edge of the Bank of the Martiers 3 leagues¹⁰ without them and lies from Cape Florida WSW 7 or 8 leagues is quite steep too, we having no ground at 50 fathom right up and down not 10 minutes before the ship was ashore and is the only dangerous place on the Florida shore and Doe assure you that from the day I got on that station, I always had the Drapsy¹¹ Line going every $\frac{1}{2}$ hour from 6 at night till daylight in the morn, the only reason I can give for finding myself on the Florida shore when I expected I was on the double Shott Bank which lies from each other SE b E and NN b N at least 16 leagues, must be occasioned by a very extraordinary and very uncommon new current; as soon as was daylight I landed all the men (but those that was employed to scuttle the decks¹² and get what water and what provisions we could, but could get but 2 butts out the whole day); at 10 o'clock this morning being Sunday we saw a small sloop when I immediately man'd and armed all the boats and sent them with orders to board her at all events and bring her here as she would be the means of carrying us off this dismal place, which I plainly saw that any common sea beat all over it and would certainly wash us all off, it being so low and dare not venture upon the main for the Indians which on this part of Florida are savages and innumerable, the next morning being Monday the boats to our great joy brought the sloop to us, the Spaniards having all deserted her, she being about 25 or 30 tuns (at most) this day was employed in getting what provisions and water we could out of the ship with what men I could get to work which was but a few, though it was for all their good but all frightened and wanted to be gone for fear of the Indians and was very rebellious and mutinous dividing into parties and growling amongst themselves

⁷ "Bilged"—stove in her planks at or below the waterline of the ship.

⁸ A ship of 44 guns on foreign service normally carried 163 barrels of gunpowder in 1781 (Montaine, Will, *The Practical Sea Gunners Companion*, p. 73, London, 1781).

⁹ The cable was 200 yards or one-tenth of a nautical mile.

¹⁰ The English and American marine league is equal to 3 nautical miles.

¹¹ Utting was speaking of the dipsey line, which is the deep-sea lead line.

¹² To cut openings in the decks.

that they was all on a footing then; and they was as good as anybody and that everything was free. I thought it was best not to take any notice but prepared for our going as soon as possible. Here I found the service of the Marines whereof which was under command and did their duty extremely well and Centenells being obliged to mount 25 Marines and 25 seamen every night, though the place so small the Indians having numbers of canoes.

Tuesday was employed getting what water we could out of the ship and putting the boats and sloop in order. Raised the long boat a strack¹³ which enabled her to carry 60 men. On Wednesday being the 8th about noon I embarked all the men (which with the "Snow" included, was 274) viz 60 in the long boat, 20 in the barge,¹⁴ 10 in the yaul¹⁵ and 184 in the little sloop not 30 tons; sent the sloop, long boat and yaul to 3 or 4 miles from the shore. After they were gone I went on board the wreck with what barrels of powder we had saved (except a little we took in each boat) and laid in proper places on the Starboard side the gun deck, that side being out the water by her heelding off to Port and proper Fewell¹⁶ in every place we could when all being laid, about 2 in the afternoon, I set her on fire and rowed off to the boats we kept in sight of her till sunset and she having blown up in several places and was in flames fore and aft but am much afraid the guns and anchors will fall into the hands of the Spaniards as they have frequent correspondence and trade with the Indians, and it is my opinion the people which left the sloop we took, were over to Cuba in a launch directly to give them intelligence. This is the fatal end of H.M.S. Loo exactly as it happened. I sent in the long boat Mr. Randall and Mr. Lloyd, my first and third Lieuts., the Master in the barge and a mate in the yaul, myself and 2 Sevts. being in the sloop which when the hold was as full of men as could possibly be stowed, the deck was the same and much in danger of oversetting if any wind. I ordered them to follow me and in case of separation to make the best of their way over to the Bahama Bank for Providence.

I carried a light for them all night but as they all outsailed me they kept so far ahead that I lost sight of them by 12 at night when I was obliged to tack and stand to the northward, which did after making the proper signal but at daylight could see nothing of them, and it blowing fresh and the sloop top heavy with men could not carry sail, so obliged to bear away and take my fate through the Gulph of Florida for any part of Carolina even for St. Augustine (if I could fetch nowhere else) rather than all be drowned which Doe assure you had very little other prospect but thank God met with exceeding good weather and arrived at Port Royall on the 13th February at night and don't in the least doubt but the boats are got safe to Providence long before this.

I had two of the best pilots on board for the Gulph of Florida in all America who insist on it there could not be a better course steered and I have been numbers of times through the Gulph and am better acquainted with that and the coast of Carolina than any part of the world and had I had the honour to have command 20 sail and steering through for all our lives, should have steered the same course or rather more northerly, which as I observed before I cannot

¹³ The addition of planks to the gunwhales of the boat increasing her capacity.

¹⁴ The commanding officers boat.

¹⁵ A heavy double-ended row boat.

¹⁶ Fuel, combustibles.

account for but by some uncommon and very extraordinary current; as fast as I can get my officers together shall send home their depositions. Some of them seem inclinable to go to the West Indies and some to the Merchant Service and some home.

I have sent home the Mate of the Watch with the Log Book and my Second Lieut. was on board the *Snow* when cast away but I should have been very happy to have found Captain Hardy¹⁷ not sailed that I might have come home directly but as I can't be now and there being a great many chances against my coming home in a merchant ship, without being carried to Spain,¹⁸ has determined me to stay here till some opportunity offers to come home in a Man-of-War or if I could possibly be indulged with a court martial in America, I shall think it the greatest favour and if found by the Court, which I hope I shall, that I have done my duty as an officer on this unforeseen unhappy affair, to me as well as to his Majesty's Service, beg their Lordships will be pleased to give me leave to rely on their goodness for my being employed again on His Majesty's service. I have enclosed the deposition of Mr. Wm. Lyford, one of my pilots who has sailed the Gulph of Florida for many years and beg their Lordships will be pleased to let somebody enquire of General Oglethorpe for his corretor.¹⁹

I am your most humble servant,
Ashby Utting.

Port Royal
15th February 1743/4.

¹⁷ Of the *Rye*, which ship had been ordered to England as convoy to merchant ships going from the Carolina colonies.

¹⁸ The risk of capture of unprotected merchant ships was very great.

¹⁹ Recommendation of Lyford.

APPENDIX C

MEMBERS OF THE CREW OF THE "LOO" ON HER LAST CRUISE

The following is a list of names of all the men and officers appearing on the paybook of the *Loo* on her last cruise. Only those marked with an asterisk were on the ship when she was wrecked.

In those days ships' crews and officers were paid only at the end of a commission period, or at the end of a cruise. Men or officers who were transferred during a cruise were given a ticket by the purser showing the pay that was due them. These tickets were supposed to be held until the payday of the ship was announced in the newspapers, when they were presented at the designated pay office and the men received their pay. In actual practice, the interval of time between the issuance of the ticket and the actual payday was so great that many sailors suffered actual want, and to obtain funds, sold their tickets at enormous discounts to speculators.

*Adam, Ervin	Quartermaster	
*Adeane, W.	Able Bodied Seaman	
Aiken, James	Able Bodied Seaman	
Allen, Thomas	Able Bodied Seaman	
Allman, John	Landsman	Deserted September 2, 1742
Anderson, James	Quarters Servant	
Angelo, Rogero	Able Bodied Seaman	
*Arthur, James	Able Bodied Seaman	
*Atkinson, Thomas	Able Bodied Seaman	
Bagster, John	Master	
*Baker, William	Able Bodied Seaman	
Balderson, William	Able Bodied Seaman and Quartermaster's Mate	Deserted October 14, 1743, in South Carolina
Ball, William	Surgeon's Mate	
Balls, Benjamin	Able Bodied Seaman	
Banke, John	Quarter Gunner	
Baptista, John	Able Bodied Seaman	Deserted November 10, 1743, at Port Royal, S. C.
Barnes, William	Able Bodied Seaman	
Barsey, Richard	Landsman	Deserted March 30, 1743, at Plymouth, England
Barsey, Thomas	2d Master's Mate	
*Bartlett, Joseph	Able Bodied Seaman	
*Basham, Charles	Gunner's Mate and Quartermaster	
Bates, John	Able Bodied Seaman	

Bates, William	Able Bodied Seaman	
*Beckworth, Francis	Able Bodied Seaman	
Belitha, Warren	1st Lieutenant	
Bennet, John	Able Bodied Seaman	Deserted November 27, 1743, at Port Royal, S. C.
Bennett, Thomas	Landsman	Deserted September 2, 1742
Benson, Moses	Able Bodied Seaman	
*Bent, John	Able Bodied Seaman	
*Berry, John	Able Bodied Seaman	Deserted December 19, 1742, at Portsmouth, England (Returned)
*Berry, Rowland	Able Bodied Seaman	
Best, W.	Master's Mate	Deserted April 13, 1743
*Biggs, Thomas	Boatswain's Servant	
*Billonge, Jacob	Able Bodied Seaman	
Birch, Robert	Carpenter	
*Bird, Richard	Able Bodied Seaman	
*Bishop, Robert	Master	
*Black, John	Able Bodied Seaman	
Blackburn, John	Able Bodied Seaman	
Blancher, Noah	Able Bodied Seaman	
Bogue, Henry	Able Bodied Seaman	
*Bond, Henry	Able Bodied Seaman and Coxswain	
Boswell, David	Able Bodied Seaman	Deserted April 6, 1743, at Plymouth, England
*Bould, William	Able Bodied Seaman	
*Bousher, Walter		
Bradshaw, John	Able Bodied Seaman	Deserted September 16, 1742, at Plymouth, England
Breamer, James	Able Bodied Seaman	Deserted October 15, 1743, in South Carolina
*Briggs, William	Able Bodied Seaman	
Briskingham, William	Servant	
*Bristoll, George	Able Bodied Seaman	
Broughton, F.	Master's Mate	
*Brown, James	Able Bodied Seaman	
*Brown, Joseph	Able Bodied Seaman and Quarter Gunner	
*Brown, Nathaniel	Able Bodied Seaman	
*Brown, Talbert	Able Bodied Seaman	
*Brown, William	Able Bodied Seaman	
*Buckley, John	Able Bodied Seaman	
*Bugless, Ralph	Able Bodied Seaman	
*Bugless, Stephen	Captain's Servant	
Bull, John	Sailing Master's Serv- ant	
Bullman, William	Able Bodied Seaman	Deserted April 13, 1743
Burdock, John	Captain's Servant	
Burns, Patrick	Able Bodied Seaman	

Burrough, John	Able Bodied Seaman	
Burroughs, John	Able Bodied Seaman	Deserted October 5, 1743 at New York
Burt, William	Midshipman	
Burthen, James	Able Bodied Seaman	
*Burton, John	Able Bodied Seaman	
*Bushnell, William	Carpenter's Mate	
Butchard, Samuel	Able Bodied Seaman	
*Butcher, Richard	Able Bodied Seaman	
Campbell, Allen	Captain's Servant	
Campbell, Edward	Corporal	
*Campbell, John	Able Bodied Seaman	
*Canton, William	Ordinary Seaman	
Carrol, Michael	Able Bodied Seaman	Deserted October 4, 1743, New York
*Carroll, John	Ordinary Seaman	
Carter, James	Able Bodied Seaman	
Carter, Samuel	Able Bodied Seaman	
Cartwright, Benjamin	Captain's Servant	
Carty, John	Able Bodied Seaman	Deserted October 13, 1743, in South Carolina
*Caunter, Henry	Steward and Ordinary Seaman	
*Chandler, Edward	Able Bodied Seaman	
*Charming, Edward	Boatswain's Mate	
Charter, William	Able Bodied Seaman	Deserted September 16, 1742, at Plymouth, England
Chippendall, Jona	Able Bodied Seaman	Deserted April 13, 1743
*Christopher, William	Able Bodied Seaman	
*Churton, James	Landsman and Able Bodied Seaman	
Collins, John	Quarter Gunner	
Compton, John	Captain's Servant	
*Conday, Richard	Able Bodied Seaman and Midshipman	
Condray, Charles	Ordinary Seaman	Deserted November 17, 1743, at Port Royal, S. C.
Conner, John	Able Bodied Seaman	
Cook, John	Gunner's Servant	
Cook, John	Ordinary Seaman	Deserted December 14, 1742
Cook, John	Able Bodied Seaman	
Cook, Thomas	Midshipman	
*Cormick, James	Able Bodied Seaman	
*Cormick, John	Surgeon's Servant	
Cormick, Michael	Able Bodied Seaman	
Cormick, William	Able Bodied Seaman	
*Couch, James	Able Bodied Seaman and Ordinary Sea-	
	man	
Courteney, F.	Clerk	

Coverley, William	Ordinary Seaman	Deserted September 2, 1742
Cowe, Peter	1st Lieutenant	
*Cowen, Philip	Able Bodied Seaman	
Cowen, William	Able Bodied Seaman	Deserted October 13, 1743, in South Carolina
*Cowey, Robert	Midshipman	
Cox, Anthony	Able Bodied Seaman	
Creese, John	Able Bodied Seaman	Deserted August 11, 1743, at Plymouth, England
*Crilly, Thomas	Ordinary Seaman	
Cross, Samuel	Captain's Servant	
*Crow, Philip	Ordinary Seaman	
*Crowley, Bryan	Able Bodied Seaman	
Cunnam, John	Able Bodied Seaman	
*Curry, John	Captain's Servant	
Davidson, Alexander	Able Bodied Seaman	
Davies, Griffith	Ordinary Seaman	Deserted October 28, 1742, at Plymouth, England
Davies, Matthew	Able Bodied Seaman	
*Davies, Thomas	Captain's Servant	
Davies, William	Cook	
Dawson, William	Able Bodied Seaman	Deserted October 4, 1743, at New York
Day, Joseph	Able Bodied Seaman	Deserted December 12, 1742, at Portsmouth, England
Deacon, J.	Able Bodied Seaman	Deserted March 30, 1743, Plymouth, England
*Dean, James	Able Bodied Seaman	
Delancy, Lawrence	Able Bodied Seaman	
*Demount, J.	Ordinary Seaman	
Dent, Digby	Captain	
*Dickson, William	Able Bodied Seaman	
Dixon, David	Able Bodied Seaman	Deserted April 13, 1743
Donnally, Sam	Able Bodied Seaman	
*Donnovan, John	Carpenter's Servant	
Douglas, David	Corporal	
Douglass, Robert	Captain's Servant	
Dove, Benjamin	Captain's Servant	
Dover, Saunders	Trumpeter	
Dowes, William	Able Bodied Seaman	Deserted December 12, 1742, at Portsmouth, England
Downing, Robert	Able Bodied Seaman	
Downing, Thomas	Able Bodied Seaman and Master's Mate	
*Dowsing, Samuel	Able Bodied Seaman	
Driscoll, John	Ordinary Seaman	
*Driscoll, William	Able Bodied Seaman	
Drisdall, Alexander	Able Bodied Seaman	Deserted April 6, 1743, at Plymouth, England
Duncan, John	Carpenter's Mate	Deserted September 10, 1742

*Duncan, William	Able Bodied Seaman	
Dunn, George	Able Bodied Seaman	
*Dunn, Matthew	Surgeon's Mate	
Dunstar, James	Able Bodied Seaman	Deserted October 5, 1743, at New York
Dyar, Anthony	Able Bodied Seaman	
*Dyer, Darby	Able Bodied Seaman	
Eades, Thomas	Landsman	Deserted September 2, 1742, at Plymouth, England
*Easton, Thomas	Able Bodied Seaman	
*Edgecombe, William	Able Bodied Seaman	
Ellis, Benjamin	Master's Servant	
*Ellory, Robert	Landsman	
Ervin, Adam		
Evans, George	Able Bodied Seaman	
Fanson, Andrew	Captain's Servant	
*Farmer, William	3d Lieutenant and 2d Lieutenant	
Farrel, James	Able Bodied Seaman	
Ferguson, Robert	Midshipman and Mas- ter's Mate	
Field, John	Able Bodied Seaman	
*Fisher, William	Able Bodied Seaman	
Fitzgerald, Morris	Able Bodied Seaman	
Fitzpatrick, Henry	Able Bodied Seaman	Deserted December 12, 1742, at Portsmouth, England
Fletcher, John	Ordinary Seaman	
*Fling, Timothy	Able Bodied Seaman	
Forrest, Richard	Able Bodied Seaman	
Forsith, William	Able Bodied Seaman	
*Forster, Randal	Able Bodied Seaman	
Fortiene, Joseph	Able Bodied Seaman	Deserted November 17, 1743, at Port Royal, S. C.
Fraser, Daniel	Able Bodied Seaman	Deserted November 27, 1743, at Port Royal, S. C.
Frost, George	Sailmaker and Mid- shipman	
*Fullmore, Henry	Boatswain	
Gally, Thomas	Master's Servant	
Gibson, George	Able Bodied Seaman	
Gilbert, Thomas	Able Bodied Seaman	Deserted April 16, 1743, at Plymouth, England
*Gilmore, Arthur	Quarter Gunner	
Gilmore, John	Able Bodied Seaman	
*Gold, William	Able Bodied Seaman	
Goldsmith, John	Ordinary Seaman	Deserted April 13, 1743
*Good, John	Surgeon's 2d Mate	
Goodsides, Abraham		
Gordon, James	Midshipman	Deserted October 8, 1742
Gordon, Robert	Midshipman	

Gorman, David	Able Bodied Seaman	
Graham, Matthew	Coxswain	
*Graham, Samuel	Able Bodied Seaman	
Grant, Henry	3d Lieutenant's Serv- ant	
*Green, Henry	Ordinary Seaman	
Gregory, Jo.	Master's Servant	
Gresham, Charles	Landsman	
Grossier, John	Landsman	Deserted September 2, 1742
Grun, Nicholas	Able Bodied Seaman	Deserted September 10, 1742
*Hallet, John	Second Gunner	
Hamilton, James	Midshipman	
Hampshire, William	Able Bodied Seaman	
Hancock, George	Able Bodied Seaman	
Hancock, John	3d Lieutenant's Serv- ant	
*Harman, William	Able Bodied Seaman	
Harris, John	Boatswain's Servant	
Harris, Richard	Pilot	
Harris, Thomas	Master's Servant	
Harrison, Theodore	Able Bodied Seaman	
Hartie, John	Ordinary Seaman	Deserted June 30, 1743, at Portsmouth England
*Hartman, Christian	Able Bodied Seaman	
*Harwood, Lewis		
*Hatch, John	2d Gunner and Master at arms	
*Hatfield, Willey	Able Bodied Seaman	
Hawkins, John	Captain's Servant	
Hawkins, John	Ordinary Seaman	
Hay, David	Master's Mate	
Hayes, Samuel	Able Bodied Seaman	
Hays, James	Able Bodied Seaman	Deserted October 13, 1743
Headley, Christian	Trumpeter (?)	
Heaver, James	Able Bodied Seaman	
Hemins, John	Midshipman	
*Henderson, James	Able Bodied Seaman	
Henry, William	Able Bodied Seaman	
Henton, John	Able Bodied Seaman	Deserted December 26, 1742
*Hickey, Thomas	Ordinary Seaman	
*Higgenson, James	Boatswain's Servant	
*Higginson, John	Quartermaster's Mate	
*Highmas, Thomas	Master's Servant	
*Hinds, Michael	Able Bodied Seaman	
*Hogg, Peter	Able Bodied Seaman	
Holliday, Richard	Able Bodied Seaman	Deserted April 13, 1743
Holmes, John	Midshipman	
*Hope, John	Quartermaster	
Horlock, Joseph	Surgeon's 2d Mate	

Horseman, Arthur	Able Bodied Seaman	Died March 24, 1742, at Plymouth, England
Hughes, John	Able Bodied Seaman	Deserted December 12, 1742, at Portsmouth, England
*Hull, Lancaster	Able Bodied Seaman and Midshipman	
Hulsal, Arthur	Able Bodied Seaman	
Hunt, John	Sailing Master	
Hunt, John	Captain's Servant	
Hussey, I.		
*Hyslop, Thomas	Armorer	
Ingerton, Dennis	Able Bodied Seaman	Deserted August 11, 1743, at Plymouth, England
Jackman, William	Ordinary Seaman	Deserted April 13, 1743
Johnson, Luke	Able Bodied Seaman	Deserted April 6, 1743, at Plymouth, England
Jolly, George	Ordinary Seaman	
*Jolly, Thomas	3d Lieutenant's Servant	
Jones, Anthony	Able Bodied Seaman	
Jones, David	Able Bodied Seaman	
Joynes, James	Quarter Gunner	
*Juba, Luke	Purser's Servant	
Julian, Charles	Able Bodied Seaman	Deserted December 19, 1742, at Portsmouth, England
Keeler, Robert	Master at Arms	
*Keighley, William	Able Bodied Seaman	
*Kelley, Morgan	Able Bodied Seaman	
Kelsey, William	Surgeon's Servant and Able Bodied Seaman	
*Kennedy, John	Able Bodied Seaman	
Kent, Ambrose		Deserted November 17, 1743, at Port Royal, S. C.
Keys, Robert	Quartermaster	
Kilrick, Isham	Able Bodied Seaman and Midshipman	
*Kilsey, William	Captain's Servant	
King, Daniel	Landsman	Deserted September 2, 1742, at Plymouth, England
*King, Nathaniel	Able Bodied Seaman	
*Kingsbury, William	Captain's Servant	
*Kirk, James	Gunner's Servant	
*Kirk, Samuel	Gunner	
*Kivey, John	Able Bodied Seaman	
*Knowles, Edward	Able Bodied Seaman	
*Knowling, James	Able Bodied Seaman	
Lake, Mark	1st Lieutenant's Servant	
Lamb, William	Quarter Gunner	

*Lander, Robert	Able Bodied Seaman	
*Langston, Richard	Quartermaster	
*Lather, Samuel	Able Bodied Seaman	
Lavermore, Joseph	Able Bodied Seaman	Deserted April 16, 1743
Lawler, John	Able Bodied Seaman	
*Ledgerwood, James	Able Bodied Seaman	
*Lemarr, Stephen	Able Bodied Seaman	
*Leslie, George	Purser	
Lewis, Christopher	Able Bodied Seaman	Deserted April 13, 1743
*Lewis, Edward	Ordinary Seaman	
Lewis, Theodore	Able Bodied Seaman	
*Lewiswentz, David	Captain's Servant	
*Limb, Giles	Able Bodied Seaman	
Linch, William	Able Bodied Seaman	
Liston, William	Ordinary Seaman	
*Lloyd, William	Midshipman	
Lobb, Thomas	Surgeon's Servant	
Lodge, John	Boatswain's Servant	
Logan, Charles	Ordinary Seaman	Deserted November 5, 1742, at Plymouth England
Long, Samuel	Able Bodied Seaman	Deserted March 30, 1743, at Plymouth, England
Long, William	Able Bodied Seaman	
Lookert, Patrick	Able Bodied Seaman	Deserted October 2, 1742
Luch, John	Able Bodied Seaman	
*Lyford, William	Able Bodied Seaman and Midshipman	
*Maby, John	Ordinary Seaman	
Malt, Issac	Able Bodied Seaman	Deserted October 3, 1743, at New York
Manley, George	Ordinary Seaman	Deserted April 13, 1743
Mannon, John	Able Bodied Seaman	
*Marriot, William	Able Bodied Seaman	
Martin, John	Able Bodied Seaman	
Maxwell, James	Quartermaster	
May, William	Ist Lieutenant's Serv- ant and Able Bodied Seaman	
*McCann, John	Able Bodied Seaman	
McCarty, Daniel	Able Bodied Seaman	
McChownley, Lott	Able Bodied Seaman	
McClelland, Robert	Able Bodied Seaman	Deserted October 4, 1743, at New York
*McClockland, William	Able Bodied Seaman	
McCowley, Charles	Ordinary Seaman	
McDugal, James	Able Bodied Seaman	
McKensie, Samuel	Quarter Gunner	
McKnight, James	Ordinary Seaman	
*McNeal, William	Quartermaster	
Meachem, James	Able Bodied Seaman	

Mellan, John	Boatswain's Mate	
Meridith, John	Ordinary Seaman	Deserted April 13, 1743
Mignam, George	Surgeon	
*Miller, James	Able Bodied Seaman	
*Miller, Nicholas	Able Bodied Seaman	
Miller, Stephen	Boatswain's Servant	
Mills, Nathan		
*Millsom, James	Able Bodied Seaman	
Mitchell, R.	Ordinary Seaman	Deserted September 2, 1742
*Molineaux, John	Ordinary Seaman and Able Bodied Sea- man	
Moore, Samuel	Yeoman	Deserted September 10, 1742, at Plymouth, England
More, Thomas	Able Bodied Seaman	
Morran, William	Able Bodied Seaman	
Morrison, John	Able Bodied Seaman	
Morrow, Hugh	Captain's Servant	
*Mortimer, Robert	Able Bodied Seaman	
Murphy, Francis	Able Bodied Seaman	Deserted August 11, 1743, at Plymouth, England
*Murphy, James	Able Bodied Seaman	
*Murphy, John		
Murphy, Patrick	Able Bodied Seaman	
Murphy, Samuel	Able Bodied Seaman	
*Nagan, James	Ordinary Seaman	
*Nelson, Robert	Able Bodied Seaman	
*Newgent, Patrick	Able Bodied Seaman	
*Newson, Richard	Able Bodied Seaman	
Nobbs, Stephen	Landsman	
Norman, Edward	Ordinary Seaman	Deserted December 29, 1743, at Port Royal, S. C.
*Norman, William	Gunner's Servant	
Northesk, Earl of	Captain	
*Nott, Ebenezer	Ordinary Seaman and Able Bodied Sea- man	
*Nuikle, Robert	Able Bodied Seaman	
Ogburne, John	Captain's Servant	
Oliver, Richard	Landsman	Deserted September 2, 1742
*Orr, Archibald	Able Bodied Seaman	
*Osbourne, William	Able Bodied Seaman	
Parker, Peter	Able Bodied Seaman	
Parr, William	Quartermaster	Deserted December 12, 1742, at Portsmouth, England
*Parrott, Samuel	Captain's Servant	
Patrick, Richard	Cook's Servant	
Patten, Hugh	Able Bodied Seaman	Deserted March 30, 1743, at Plymouth, England
Pearse, Samuel	Able Bodied Seaman	Deserted April 16, 1743

*Pearson, Thomas	Ordinary Seaman and Able Bodied Sea- man	
Pegan, Roger	Able Bodied Seaman	Deserted November 27, 1743, at Port Royal, S. C.
Pegan, Thomas	Able Bodied Seaman	
Pelican, John	Able Bodied Seaman	Deserted March 17, 1742, at Plymouth, England
Pemell, Thomas	Able Bodied Seaman	
*Peters, William	Able Bodied Seaman and Midshipman	
Phallem, Edmund	Able Bodied Seaman	
*Phillips, Thomas	Cook	
*Phonix, Philip	Able Bodied Seaman	
*Pickering, Michael	Clerk	
*Plantain, Charles	Able Bodied Seaman	
Poole, Thomas	Pilot	
Potterfield, George	Able Bodied Seaman	
Powell, Philip	Able Bodied Seaman	Deserted March 30, 1743, at Plymouth, England
Pownswell, Edward	Able Bodied Seaman	Deserted December 12, 1742, at Portsmouth, England
*Pretty, Thomas	Able Bodied Seaman	
*Price, James	Able Bodied Seaman	
*Priest, Lewis	Able Bodied Seaman	
Puttick, William	Able Bodied Seaman	
*Quaco, John	Captain's Servant and Ordinary Seaman	
*Quin, John	Able Bodied Seaman	
Ramsey, Patrick	2d Gunner	
*Randall, James	2d Lieutenant and 1st Lieutenant	
*Randall, James	Able Bodied Seaman	
*Randall, John	Able Bodied Seaman and Midshipman	
Randell, James	1st Lieutenant	
*Randolph, J.	Able Bodied Seaman and Master's Mate	
*Ratsey, George	Cooper and Able Bod- ied Seaman	
Reed, Thomas	Able Bodied Seaman	Deserted October 6, 1743, at New York
*Rhode, John	Able Bodied Seaman and Ordinary Sea- man	
*Richards, Nicholas	Able Bodied Seaman	
*Richardson, William	Able Bodied Seaman	
Richey, David	Quartermaster's Mate	
*Richmond, Andrew	Able Bodied Seaman	
*Rider, Charles	Able Bodied Seaman	

Risden, Joseph	Able Bodied Seaman	
Roach, Henry	Able Bodied Seaman	Deserted December 12, 1742, at Portsmouth, England
Roberts, David	Ordinary Seaman	Deserted October 28, 1742, at Plymouth, England
Roberts, Edward		Deserted December 19, 1742, at Portsmouth, England
Roberts, John	Sailmaker's Mate	
Roberts, John	Captain's Servant	
Roberts, Joseph	Captain's Servant	
*Roberts, William	Captain's Servant	
Robinson, Alexander		
Robinson, John	Able Bodied Seaman	
Rogers, Robert	Landsman	Deserted September 2, 1742
Rowe, Edward	Able Bodied Seaman	
Rowe, George	Quarter Gunner	Deserted December 12, 1742, at Plymouth, England
Rowe, Peter	Able Bodied Seaman	Deserted October 4, 1743, at New York
Royall, James	Able Bodied Seaman	
*Russell, Richard	Boatswain's Servant	
Ryan, John	Able Bodied Seaman	Deserted September 10, 1742, at Plymouth, England
St. Lawrence, Samuel	Ordinary Seaman	Deserted April 13, 1743
Salisbury, Edward	Able Bodied Seaman	
*Salmon, Joseph	1st Captain's Servant	
*Salter, James	Able Bodied Seaman	
*Saunders, Joseph	Able Bodied Seaman	
Scannel, John	Able Bodied Seaman	
Scott, George	Gunner	
Scott, Richard	Landsman	
*Shaw, Patrick	Able Bodied Seaman	
*Shearing (John or Joseph)	1st Lieutenant's Serv- ant and 3d Lieuten- ant's Servant	
*Shearing, Thomas	Able Bodied Seaman	
Sherwood, William	Able Bodied Seaman	
Shirley, Washington	3d Lieutenant	
*Shoart, Oliver	Able Bodied Seaman	
Simmonds, Richard	Quarter Gunner	Deserted April 6, 1743, at Plymouth, England
*Simms, James	Ordinary Seaman	
Singleton, William	Ordinary Seaman	Deserted September 2, 1742
*Skinner, Philip	Ordinary Seaman	
Sluman, John	Gunner	
Smith, Benjamin	Able Bodied Seaman	
*Smith, James	Able Bodied Seaman	
Smith, Paul	Servant	
Smith, Theodore	Boatswain's Servant and Able Bodied Seaman	Deserted October 4, 1743, at New York

Softley, Robert	Able Bodied Seaman	Deserted March 30, 1743, at Plymouth, England
Somerwel, Joseph	Able Bodied Seaman	Deserted April 13, 1743
Southard, Thomas	Able Bodied Seaman	Deserted September 10, 1742, at Plymouth, England
Spare, Thomas	Able Bodied Seaman	
Sparks, Joseph	Able Bodied Seaman	
*Spinks, Stephen		
Spry, Nicholas	Able Bodied Seaman	Deserted March 17, 1742, at Plymouth, England
Stanford, Richard		
Stapleton, A.	Quartermaster's Mate	
Stephenson, James	Landsman	Deserted September 2, 1742, at Plymouth, England
*Steuart, Neil	Surgeon	
Stevenson, Henry	Able Bodied Seaman	Deserted October 15, 1743, in South Carolina
Stewart, Alexander	Able Bodied Seaman	
*Stiveash, Stiven	Able Bodied Seaman	
*Stoneham, John	Able Bodied Seaman	
Stradder, Forbel	Landsman	Deserted April 13, 1743
Stroud, John	Boatswain	
*Sullivan, Thomas	Ordinary Seaman	
Swain, William	3d Lieutenant's Serv- ant and Captain's Servant	
*Sweeny, Daniel	Able Bodied Seaman	
*Swickman, Thomas	Landsman	
Swift, Theodore	Able Bodied Seaman	Deserted August 5, 1743, at Portsmouth, England
*Tabler, Thomas	Captain's Servant and Able Bodied Sea- man	
*Taylor, John	Carpenter's Servant and Able Bodied Seaman	
*Taylor, Jonathan	Able Bodied Seaman	
*Taylor, William	Captain's Servant and Ordinary Seaman	
Thatcher, John	Quartermaster	
*Thompson, Richard	Pilot	
Thoyer, Peter	Able Bodied Seaman	
*Tipper, John	Able Bodied Seaman	
Toby, George	Able Bodied Seaman	Deserted October 6, 1743, at New York
Todd, Alexander	Able Bodied Seaman	Deserted March 30, 1743, at Plymouth, England
*Torginton, Joseph	Carpenter's Servant	
Treacey, William	Able Bodied Seaman	Deserted December 26, 1742, at Portsmouth, England

*Triming, Thomas	Able Bodied Seaman	
*Trist, Nathaniel	Able Bodied Seaman	
Trott, Thomas	Able Bodied Seaman	
Trotter, Benjamin	Able Bodied Seaman	
Trouve, Paul	3d Lieutenant's Serv- ant	
*Trunker, William	Able Bodied Seaman	
Tunis, Michael	Able Bodied Seaman	
Turford, Thomas	Carpenter	Deserted September 10, 1742, at Plymouth, England
*Utting, Ashby	Captain	
Vincent, Aaron	Able Bodied Seaman	
*Vivian, John	Carpenter	
*Wadlin, Richard		
*Walker, James	Ordinary Seaman	
Walker, John	Able Bodied Seaman	Deserted October 2, 1742, at Cork, Ireland
Walker, Peter		Deserted December 12, 1742, at Portsmouth, England
Wallis, Benjamin	Able Bodied Seaman	Deserted September 16, 1742, at Portsmouth, England
Warceys, Thomas		
*Ward, Samuel	Able Bodied Seaman	
*Weatherill, John	Able Bodied Seaman	
Wedlock, John	Able Bodied Seaman	Deserted December 12, 1742, at Portsmouth, England
Welch, Michael	Able Bodied Seaman	
Welsh, Peter	Ordinary Seaman	
*Wemuss, Robert	Cook's Servant	
Wemy, James	Able Bodied Seaman	
Wheeler, Robert	Able Bodied Seaman	
*White, Richard	Able Bodied Seaman	
*White, Robert	Able Bodied Seaman	
Whitver, Thomas	Able Bodied Seaman	
Wilkinson, Edward	Able Bodied Seaman	
*Williams, Richard	Able Bodied Seaman	
*Willmot, Theodore	Able Bodied Seaman	
Wills, J.		
Wilson, George	1st Lieutenant's Serv- ant	
Wilson, Lawrence	Able Bodied Seaman	
Wise, John	Able Bodied Seaman and Midshipman	
Woodgate, William		
*Wotton, William	Able Bodied Seaman	
Wright, William	Able Bodied Seaman	Deserted September 23, 1742, at Plymouth, England
*Yeates, James	Captain's Servant	
*Young, John	Ordinary Seaman	
Younger, John	Captain's Servant	

MARINE LIST

Colonel Cotterel's Regiment :

*Allen, Robert

Baker, John

Deserted December 26, 1742,
at Portsmouth, England

*Ball, William

*Bond, George

*Brooke, Joshua

*Brooks, George

Brooks, John

Brown, George

Brown, John

Cant, Thomas

Clint, Richard

*Cole, Joseph

*Cook, Samuel

Corbett, Thomas

Diamond, Robert

*Dight, Edward

*Douglass, Edmund, Sergeant

Drake, Richard

*Farries, William, Sergeant

Finch, Samuel

*Fitzsimmons, Thomas

*Gaddish, Lazarus

*Gleddon, Richard

*Gould, William

Grovenor, Francis

Deserted June 30, 1743, at
Portsmouth, England

Hall, William

*Hardeman, William

*Harding, Matthew

*Haydon, Timothy

Hodge, Hugh

Deserted December 12, 1742,
at Portsmouth, England

*Hold, Thomas

Hughes, Edward

*Hyatt, Samuel

Isaac, Titus

Johnson, Adam

*Jones, Philip

*King, Joshua

Lee, John

Martin, Thomas

*Matthews, Joseph

*McCraw, Daniel

Miller, Richard

Deserted December 2, 1742,
at Portsmouth, England

Mitchell, John

- *Morgan, John
- *Morgan, William
- *Mould, Thomas
- *Murray, Peter
- *Overshott, John
- Pearce, George
- Phillips, Edward
- Phillips, William
- Prest, Timothy
- *Ridgheboth, Thomas
- *Ridsen, Samuel
- Roberts, John
- Rowls, John
- Searle, John
- Short, George
- Spraeg, Nicholas
- *Stevens, Samuel
- *Stone, John
- Thrasher, John
- *Toll, John
- Trovana, William
- *Turner, Jonas
- *Turpin, John
- *Vaughan, Hector, Lieutenant
- *Walker, William
- Whiteker, Thomas
- *Williams, Thomas
- Wills, Samuel
- *Woodeson, John
- Woodley, Nicholas
- Colonel Wynyard's Regiment
- Aldridge, William
- Chappel, Samuel
- Clayton, Joseph
- Hancock, Justinian
- Hope, Richard
- *Kent, Benjamin
- *Korgett, John
- Parker, Daniel
- *Stokes, William
- *Trowes, Richard
- *Wright, Samuel

APPENDIX D

ROSTER OF THE FAMILY AND SERVANTS OF GEORGE CLINTON, GOVERNOR OF NEW YORK FROM SEPTEMBER 1743 TO OCTOBER 1753, PASSENGERS ON THE "LOO" DURING HER LAST VOYAGE TO AMERICA, AUGUST-SEPTEMBER 1743 ¹

Clinton, Ann (Governor's wife)	Cunningham, Archibald
Clinton, Ann	Davies, Ann
Clinton, George (Governor)	Ellis, Thomas
Clinton, Henry	Fenton, Sarah
Clinton, Lucy	Harvey, Phillip
Clinton, Mary	Ryves, James
Ascough, John	Vanham, John
Aurneo, Ann	White, Margaret
Blundell, Christopher	Williams, William
Catherwood, John	Willson, Ann

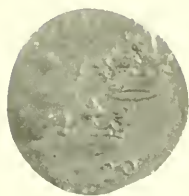
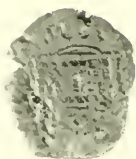
¹ Based on the Muster Roll of the *Loo*, ADM 36, vol. 1823.

APPENDIX E

COMMANDING OFFICERS OF THE "LOO"

1. Harland, Robert	April 4, 1707–October 1, 1709
2. Herbert, Jona	October 1, 1709– ?
3. Walrund, Beau	1709– 1715
4. Splain, Tim	April 1717(?)–December 1717
5. Protherie, George	April 1718– 1720
6. Scott,—(Captain)	October 1720– 1722
7. Waterhouse, Tho. (Commodore)	February 1727/28–October 1728
8. Lee, FitzHenry	October 22, 1728–April 2, 1729
9. Berkeley, William	April 2, 1729– ?
10. Best, John	May 5, 1735–May 1737
11. Northesk, Earl of	January 4, 1741/42–September 1742
12. Dent, Digby	September 17, 1742–April 11, 1743
13. Utting, Ashby	April 11, 1743–February 5, 1743/44

¹ Based on the Navy List, 1707-1744.



1. Copper coins recovered from the wreck site of the *Loo* in the summer of 1950. Left to right: Spanish 8 maravedi circa 1600, Spanish 8 maravedi circa 1640, and Swedish $\frac{1}{2}$ ore dated 1720. This last coin was important evidence in dating the wreck. Lent to the U. S. National Museum by Dr. and Mrs. George Crile, Jr.



2. Small Queen Anne pewter teapot from the wreck of the *Loo*. Gift to the National Museum from E. A. Link. The pot was damaged by fire when the *Loo* was burned by her captain after being wrecked.



The salvage boats of the expedition at anchor over the wreck site. The remains of the ship lay between two coral reefs in 35 feet of water. (Photograph by Dr. George Crile, Jr.)



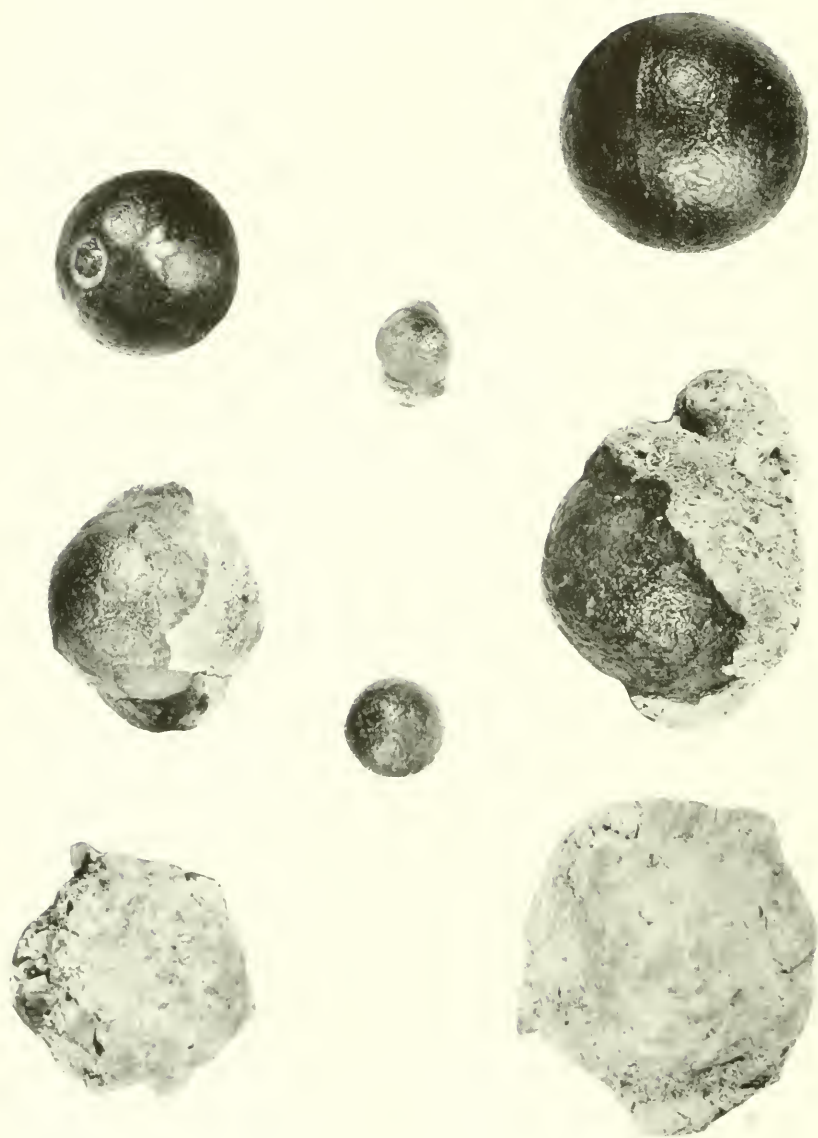
The ring of one of the *Loo's* bower anchors protruding from the coral. Note the coral-sand encrustation that covers the ring and the end of the anchor shaft. (Photograph by Dr. George Crile, Jr.)



Divers working on the wreck site. The diver in the center is washing the sand bottom with a jet of water to uncover small objects. Dr. George Crile, Jr., at the left, is taking underwater motion pictures. (Photograph by Mrs. George Crile, Jr.)



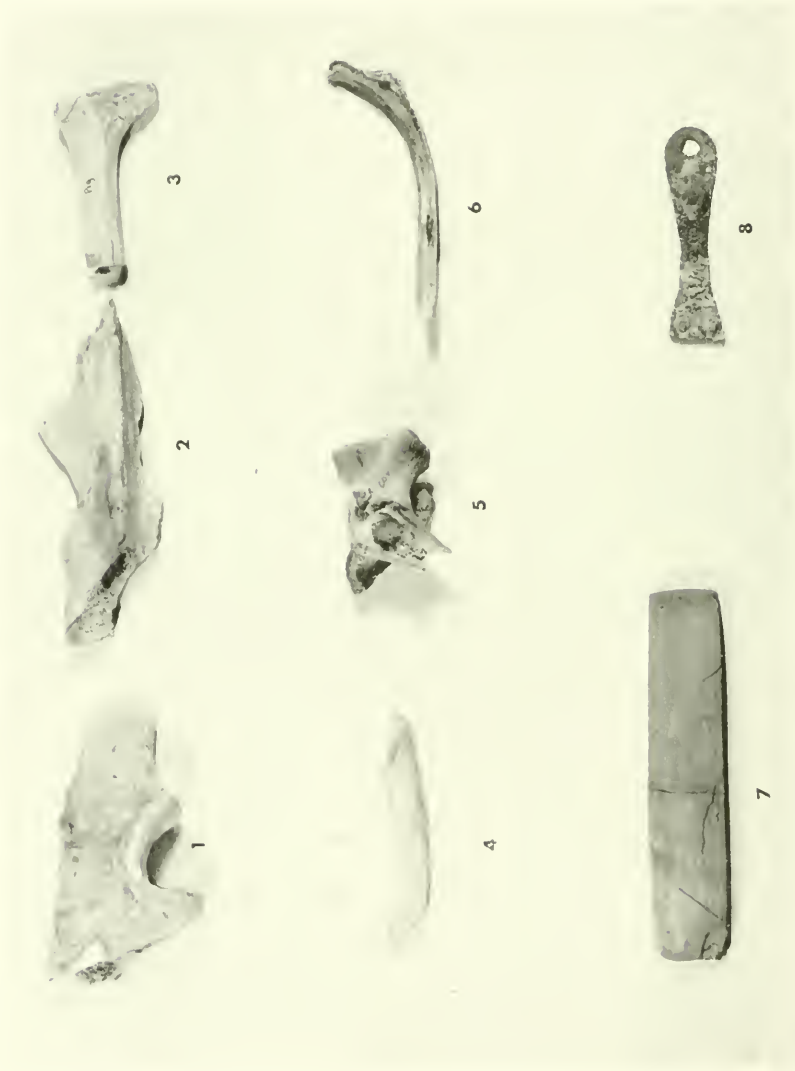
A basket of coral-sand-encrusted shot coming up from the bottom.
(Photograph by Dr. George Crile, Jr.)



Cast-iron shot recovered from the site of the wreck of the *Loo*. Top: 6-pound shot, coral-sand-encrusted and cleaned; note the broad arrow. Center: Left, 1-pound shot, a single grape for a 12-pounder or shot for a 1-pounder swivel gun; right, 1/2-pound shot, a single grape for a 6-pounder or shot for a 1/2-pound swivel gun. Bottom: 12-pound shot, coral-sand-encrusted and cleaned, marked with the broad arrow.



Ceramic materials recovered from the wreck site : 1, Two fragments of English salt-glaze stoneware, blue decoration. 2, Bottom portion of a dark-green glass spirit bottle. 3, Fragments of Chinese porcelain, blue decoration. 4, Neck of a dark-green glass spirit bottle. 5, Fragment of Chinese porcelain embedded in a lump of coral. 6, Bottom portion of a dark-green glass spirit bottle. 7, Another, attached to a lump of coral.



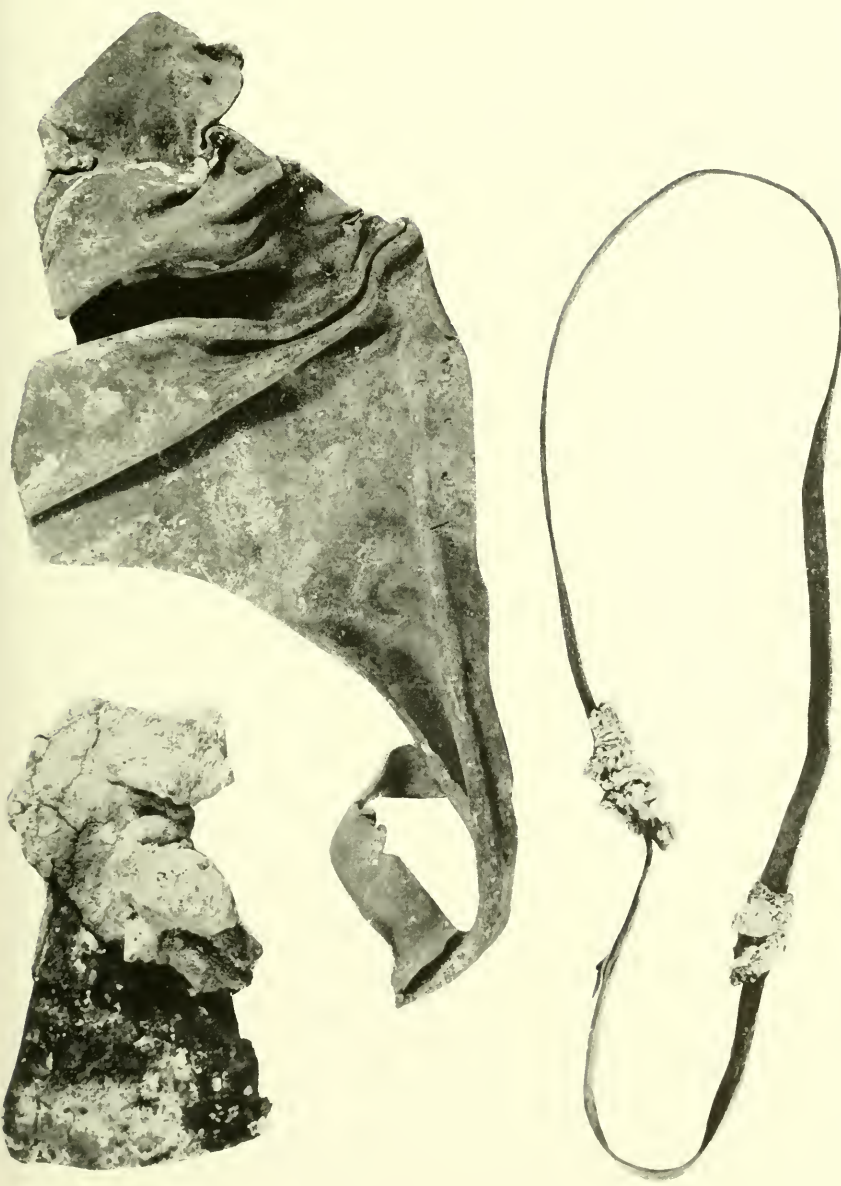
Objects recovered from the wreck site: 1, 2, 4, 5, and 6, Cow bones from the salt-meat stores of the ship. 3, Pig bone. 7, Sharpening stone; note marks left by a blade on the left end of the stone. 8, Brass pot handle.



James Rand holding a portion of a pig's jaw from the remains of the salt-meat stores of the ship.
(Photograph by Mrs. George Crile, Jr.)



Objects recovered from the wreck site: 1, Wrought-iron brace, exact use unknown. 2, Eye-bolt from the ship's standing rigging. 3, Wrought-iron hull bolt. 4, Lead pipe, probably a scupper or hawse pipe. 5, Iron door lock. 6, Lump of coal. 7, Wrought-iron hook from the rigging.



Objects recovered from the wreck site: Top, left, coral-sand-encrusted broadax ; right, sheet lead from a hull repair.
Bottom, brass hoop from a cask or tub, marked with the broad arrow.



E. A. Link rigging the main boom of the *Blue Heron* to raise a 1-ton iron barrel from the wreck site. (Photograph by Mrs. George Crile, Jr.)



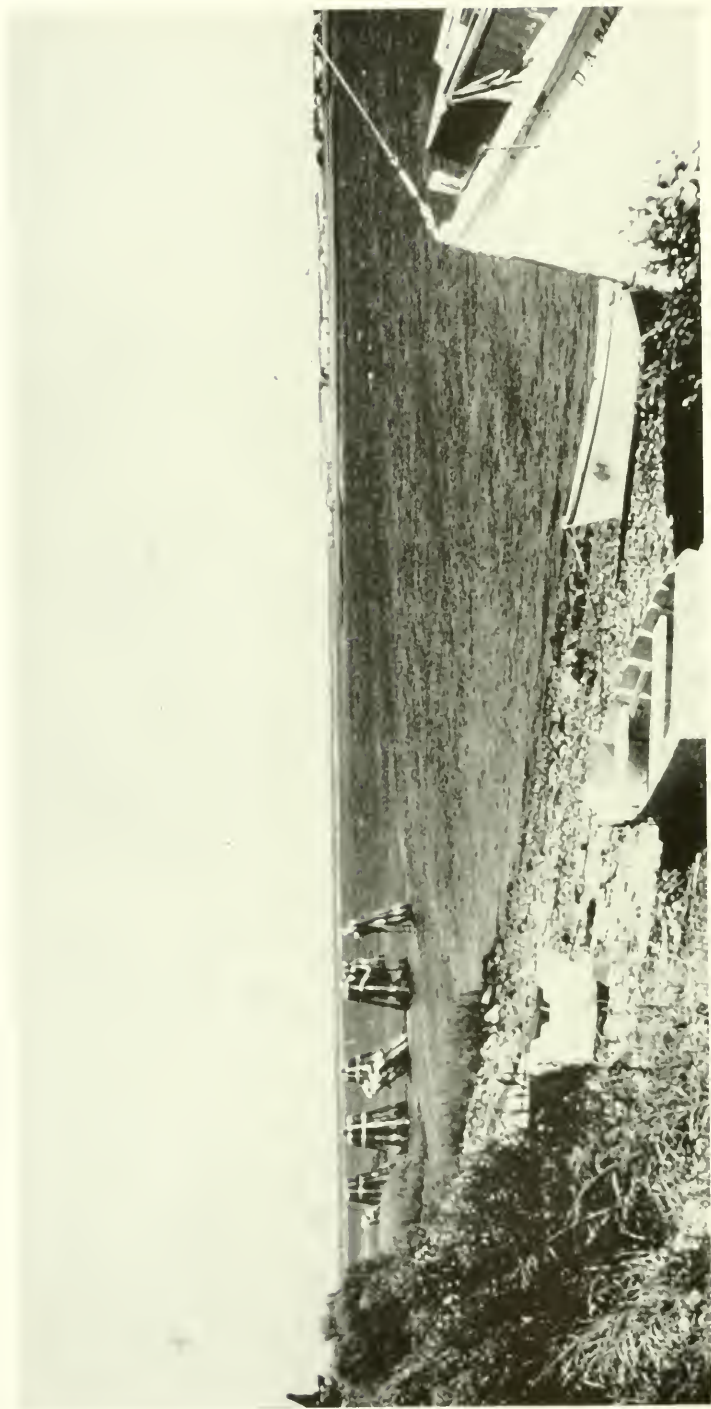
A coral-sand-encrusted iron 6-pounder from the *Loo* being unloaded from the *Blue Heron* at Marathon, Fla.
(Photograph by Dr. George Crile, Jr.)



Coral-sand crust falling away from an iron 6-pounder. (Photograph by Mrs. George Crile, Jr.)



Long 6-pounder from the *Loo*, after coral-sand coating was removed. (Photograph by Mrs. George Crile, Jr.)



Port Royal harbor as it appears today. Capt. Utting and 160 survivors of the wreck of the *Loo* arrived here February 13, 1744, aboard a captured Spanish sloop.

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SYNONYMICAL NOTES ON NEOTROPICAL
FLIES OF THE FAMILY TABANIDAE
(DIPTERA)

By

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Gorgas Memorial Laboratory, Panama



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SYNONYMICAL NOTES ON NEOTROPICAL FLIES OF THE FAMILY TABANIDAE (DIPTERA)¹

By G. B. FAIRCHILD

Gorgas Memorial Laboratory, Panama

The nomenclature of the Neotropical flies of the family Tabanidae has long been in a state of great confusion, in spite of the efforts of a number of students to bring it into some sort of order. The main difficulties seem to have been the lack of adequate collections in any one place and the very numerous inadequate descriptions by several of the older authors. The existing catalogs of Kertész (1900, 1908) and Surcouf (1921) for the Tabanidae of the World are quite uncritical and are chiefly lists of names. The catalog of the Neotropical Tabanidae prepared by Kröber (1934) was a great step forward, but subsequent work has modified greatly the understanding of generic and higher categories, and he failed in many cases to appreciate the value of a study of the type specimens of the older descriptions. His catalog, therefore, although extremely useful, has often proved unreliable.

During the fall of 1953 I was enabled, through the aid of a generous travel grant from the Marsh Fund of the National Academy of Sciences, to visit the British Museum in London and the Muséum d'Histoire Naturelle in Paris. The trip was undertaken for the purpose of studying and comparing specimens with the types of Neotropical Tabanidae (horse flies and allies) contained in the collections of the British Museum in London and the Muséum d'Histoire Naturelle in Paris. The Neotropical species of Tabanidae described by Francis Walker between 1848 and 1860, by M. J. Macquart between 1834 and 1855, and by J. M. F. Bigot in 1892 have been a serious stumbling block to students for many years. Not only did these three authors among them describe some 300 species, but their descriptions were, for the most part, so superficial and inadequate that a large proportion of their names have remained unrecognized or misinterpreted. Furthermore, some 27 generic names have been based on these species, often without adequate knowledge of their characters. Although the primary

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purpose of the trip was to study the type specimens of these three authors, most of which are deposited in either London or Paris, it was felt important to examine all other types of Neotropical Tabanidae available in these two institutions.

Since time would not permit the careful description and drawing of all the species likely to be found, it was felt of utmost importance to take over for comparison specimens of as many species as possible. Through the courtesy of the authorities of the Museum of Comparative Zoology at Cambridge, Mass., and of the U. S. National Museum, a collection of nearly 600 species of Neotropical Tabanidae was secured and taken to London and Paris.

Although not a few of the types I had hoped to see have been lost or destroyed in the course of the nearly 100 years since they were described, I was fortunate in being able to see a good many additional species of more recent date which I had not expected to find. These included a number of the types of species described by Osten Sacken, Williston, Townsend, Surcouf, Ricardo, Summers, and Kröber. I was able to bring back specimens matched with the types of about 220 Neotropical species, fairly complete notes, in some cases with drawings, on a further 107 types, and miscellaneous notes on an additional 60 to 70 species, not types, of which I had not previously seen specimens.

It is a pleasure to acknowledge my indebtedness to Dr. Alexander Wetmore of the National Academy of Sciences, who facilitated the procuring of travel funds, and to Dr. Joseph Bequaert and Dr. Alan Stone for their generosity in lending material in the collections under their care. Capt. N. D. Riley, C. B. E., Keeper of Insects at the British Museum, most generously placed the facilities of that institution at my disposal; and I am most especially grateful for the invaluable help and cordial hospitality of H. Oldroyd and Paul Freeman of the Diptera section of the Museum. At Paris, M. E. Seguy, custodian of the Diptera section in the Muséum d'Histoire Naturelle, put the collections at my complete disposal and did everything possible to make my short stay pleasant and profitable. The drudgery of taking dictation and typing the extensive notes fell to my wife, without whose invaluable assistance the work could not have been completed.

The Tabanidae at the British Museum are arranged primarily on a taxonomic basis, the various groups following one another irrespective of locality. Each drawer is marked with the genera it contains and a colored slip indicating the geographical regions represented. There is also a card catalog of the species in the collection. All types are incorporated in the general collection but are marked with small circular

labels, usually red for primary types, green for cotypes, and yellow for paratypes.

In its present state, the arrangement and labeling are largely the work of E. E. Austen, the late curator, and H. Oldroyd, the present curator. Austen is largely responsible for verifying Walker's types, which, until his time, were not marked as such. The Bigot collection, containing Macquart and Bigot types, was remounted on double mounts after receipt by the British Museum. In most cases only one specimen of a series bore a label—those of Macquart which Bigot had pasted onto larger labels, or his own folded and often much defaced labels. In repinning this material great care seems to have been taken to put the labels back on the same specimens, though in one or two cases there appears to have been an exchange of labels. Mr. Oldroyd has done the great service of marking all the types with distinctively colored labels, a procedure that greatly facilitated their recognition.

At Paris, the collections are housed in large glass-topped cardboard boxes. There has been no effort to rearrange the Tabanidae, and the collection is really a series of separate collections. Although most of the Tabanidae are together, the Macquart collection is in its own series of boxes, not mixed with subsequent additions. Surcouf's material is also separate. This policy seems the only sound one under the prevailing conditions, as M. Seguy is in charge of several other orders besides Diptera, and has but one assistant. The Meigen collection of Diptera, as well as several other largely European collections, is thus preserved. For the most part, the Macquart types are not labeled as such and bear only their original labels, so that reference to the original descriptions is often necessary. The box labels under which the species stand are, I believe, a later addition, and are not very helpful or consistent. Since most of the specimens are types or easily recognized species, determination as to which specimen is a type is usually not difficult. The Macquart collection is also divided geographically, the Neotropical, Nearctic, etc., species placed together. Owing to lack of realization that Mexican material may have been considered Nearctic, I quite likely missed seeing the types of several of Macquart's species, as I lacked time to go through other than the Neotropical boxes.

Most of Walker's Neotropical species were described in the "List of the Specimens of Dipterous Insects in the Collection of the British Museum," which is here abbreviated to "List" with volume, page, and year. His other publications are more fully cited. Macquart's species appeared mostly in a series of articles entitled "Diptères Exotiques Nouveaux ou Peu Connus," here abbreviated to "Dipt. Exot." This

series appeared more or less simultaneously in the *Mémoires de la Société Royale des Sciences, de l'Agriculture et des Arts de Lille*, and in a separately published form put out by Librairie Encyclopédique de Roret, Paris. There is no difference in the text, but the pagination is different, and in some cases the reprint is of an earlier or later date. I have not been able in all cases to check as to which edition a given page number refers, but since the work is adequately indexed in both editions, this is not of great importance. The possible conflict between Supplement 4 of Macquart's work and the *Diptera Saundersiana* of Walker, both dated 1850, does not seem to concern any names for Neotropical Tabanidae. Mr. Oldroyd felt that since Macquart's paper was read in June 1849, though not published until sometime in 1850, while Walker's paper appeared after September 12, 1850, it is best to assume priority for Macquart's names where conflict occurs. Nearly all of Bigot's species were described in an article entitled "Descriptions de Diptères Nouveaux" published in 1892 in *Mém. Soc. Zool. France*, vol. 5, and will be cited here merely by the date and page. Secondary references will be cited only by author and date, the full reference cited only in the bibliography.

Although fairly detailed notes, and in some cases camera lucida sketches, of nearly all the types examined were made, it has seemed better to present the results in the more condensed form of an annotated list of the types examined. Much information that might aid in the determination of specimens has thus had to be omitted, and the list is primarily of nomenclatorial interest. It is planned, as time and opportunity permit, to make the more interesting and perhaps more valuable descriptive matter of the notes available, together with figures of homotypes, in connection with planned revisionary studies now being undertaken in collaboration with Dr. C. B. Philip. In the meantime, copies of the full notes will be deposited in the U. S. National Museum and the British Museum for reference purposes.

I have refrained from specifically selecting lectotypes of species with more than one specimen in the type series. To do so at the time of examination would have used more time in writing labels than I could spare; to do so now would lead me into explanations and justifications for my action in each case and would unduly lengthen this paper. In cases where more than one species is obviously involved in the type series, I have indicated which one I believe should represent the name.

The species discussed here are nearly all listed by Kröber (1934) in his catalog of the Neotropical Tabanidae. A few species listed by him have been omitted here, such as *T. pruinosis* Bigot from Mexico, fully treated by Philip (1950), and *T. parvidentatus* Macquart, dis-

cussed by Bequaert (1940). Several other names are Nearctic and cataloged by Philip (1947). Names omitted by Kröber are so indicated here, except in the case of those originally published with no locality or a non-Neotropical locality.

The type material of the following 64 species was not found either in London or Paris. The species are listed below alphabetically, with place and date of publication, locality, and collection as originally given where this information is available to me. Several names are homonyms and so indicated. Species for which no locality was originally given, or where the author states his ignorance of the provenance of the specimen, are indicated by "Loc.?" In many cases these species may not have been Neotropical, and in the case of the collection at Paris, no search of the Old World or Nearctic collections was made for them. In London, the card catalog of types was checked, and so it is reasonably certain that Walker's species now missing from the collections are truly lost. In some cases additional notes on status have been added.

Dichelacera abicens Wlk. 1848, List, 1: 191. West Indies, B. M. Seen by Ricardo (1904) but subsequently lost (Bequaert, 1940).

Tabanus advena Wlk. 1850, Newman's Zoologist, 8, App., p. lxix. Loc.? B. M.

Tabanus albiscutellatus Macq. 1850, Dipt. Exot., Suppl. 4: 34. Mexico = *leucaspis* Wied. (Osten Sacken, 1878; Kröber, 1934; Fairchild, 1941). Perhaps in Nearctic coll.

Tabanus albivittatus Macq. 1834, Hist. Nat. Dipt., 1: 206. Loc.? Coll. Percheron. Probably not Neotropical. *T. albivittatus* Schuurm. Stekh. 1926 is a homonym.

Pangonia ardens Macq. 1838, Dipt. Exot., 1(1): 197. Saint Leopold. Coll. Serville.

Tabanus argentifrons Wlk. 1848, List, 1: 186. Loc.? B. M.

Pangonia bicolor Macq. 1850, Dipt. Exot., Suppl. 4: 27. Mexico = *Esenbeckia semiflava* Wied. (Bellardi, 1859; Kröber, 1934). Homonym of *P. bicolor* Macq. 1846. New Holland.

Haematopota bivittata Macq. 1834, Hist. Nat. Dipt., 1: 212. Amer. Merid. = *Diachlorus bivittatus* Wied. 1828 (Kröber, 1934). From description, a *Diachlorus*, though not credited to Wiedemann in original description.

Tabanus bivittatus Macq. 1845, Dipt. Exot., Suppl. 1: 35. Brazil. Coll. Spinola.

Tabanus bonariensis Macq. 1838, Dipt. Exot., 1 (1): 142. Buenos Aires. Coll. Serville. Kröber (1934) places in *Agclanius* with *acupunctatus* Rond. 1868, as synonym.

Tabanus brevivitta Wlk. 1850, Newman's Zoologist, 8, App., p. xcvi. Loc.? B. M. Homonym of *T. brevivitta* Wlk. 1848. Australia.

Tabanus castaneus Macq. 1834, Hist. Nat. Dipt., 1: 198. Cayenne. The description indicates probable synonymy with *T. unicolor* Wied.

Tabanus castancoenensis Macq. 1838, Dipt. Exot., 1 (1): 152. Loc.? Mus. Paris.

Tabanus chrysolenus Wlk. 1854, List, 5, Suppl. 1: 327. Brazil. B. M.

Tabanus despectus Kröber 1930, Dipt. Pat. S. Chile, 5 (2): 158. Chile. B. M. (Paratype.) This and several other species described in same paper appear

not to have been returned to B. M. by Kröber. *T. despectus* Fchld. 1942 is a homonym, but proposal of a replacement name now seems unnecessary, as the species is uncertainly distinct.

Tabanus dorsivitta Wlk. 1850, Dipt. Saund., 1:39. S. America? B. M. The African *T. dorsivitta* Wlk. 1854 is a synonym of *T. taciola* P. de B.

Tabanus flammans Wlk. 1848, List, 1:153. Loc.? B. M.

Tabanus flavibarbis Macq. 1845, Dipt. Exot., Suppl. 1:169. Cayenne. Coll. Spinola. Kröber (1930h) claims to have seen the type and places *guyanensis* Macq. as a synonym. The latter has, however, page priority.

Tabanus flavifascies Macq. 1845, Dipt. Exot., Suppl. 1:36. Colombia. Coll. de Brene.

Tabanus formosus Wlk. 1848, List, 1:148. Loc.? B. M.

Chrysops frontalis Macq. 1838, Dipt. Exot., 1 (1):160. Saint Domingue. Collection not stated.

Tabanus fullo Wlk. 1850, Newman's Zoologist, 8, App., p. lxxvii. Loc.? B. M.

Chrysops fulviceps Wlk. 1854, List, 5:285. Pará. B. M. The description agrees best with *C. incisa* Macq. Ricardo (1901) says type could not be found at B. M.

Tabanus fulvifasciatus Macq. 1834, Hist. Nat. Dipt., 1:206. Loc.? Coll. Percheron.

Tabanus fulviger Wlk. 1850, Dipt. Saund., 1:65. Loc.? B. M.

Chrysops geminata Macq. 1850, Dipt. Exot., Suppl. 4:39. Mexico. The name is a homonym of *geminata* Wied. and a presumed synonym of *virgulatus* Bell. 1859.

Tabanus gigas Macq. 1834, Hist. Nat. Dipt., 1:200. Loc.? A homonym of *T. gigas* Herbst 1787.

Pangonia hebes Wlk. 1848, List, 1:137. Loc.? B. M. Ricardo (1901) says type lost, but see Oldroyd (1954). Probably Australian.

Tabanus hispidus Wlk. 1850, Dipt. Saund., 1:63. Loc.? B. M.

Tabanus honestus Wlk. 1850, Dipt. Saund., 1:64. Loc.? B. M. Lutz (1907) lists as possible synonym of *fuscifasciatus* Macq.

Pangonia inconspicua Wlk. 1848, List, 1:137. Loc.? B. M. Ricardo (1901) records as missing from B. M. Coll.

Esenbeckia insignis Kröber 1931, Zool. Anz., 94:255. Brazil. B. M.

Tabanus lageniferus Macq. 1838, Dipt. Exot., 1 (1):148. Loc.? Mus. Paris.

Tabanus longifrons Kröber 1930, Dipt. Pat. S. Chile, 5 (2):152. Chile. B. M. Apparently not returned by Kröber.

Tabanus longipennis Macq. 1834, Hist. Nat. Dipt., 1:201. Loc.? Coll. Percheron.

Chrysops lugubris Macq. 1846, Dipt. Exot., Suppl. 1:44. Brazil. Coll. Robyns, Bruxelles. The description suggests possibility that this was not a *Chrysops*.

Tabanus maculipennis Macq. 1834, Hist. Nat. Dipt., 1:198. Brazil. Coll. Serville. A homonym of *T. maculipennis* Wied. 1828, and Brullé 1832. Not same as *maculipennis* Macq. 1846. Not listed by Kröber (1934).

Tabanus maculipennis Macq. 1846, Dipt. Exot., Suppl. 1:34. Brazil. Coll. Spinola. A homonym of *maculipennis* Wied. 1828, and Macq. 1834, but a different species, probably a synonym of *Tabanus (Hybomitra) quadripunctata* and the genotype of *Dasyphyra* End. (Kröber 1934).

Tabanus marginenevris Macq. 1855, Dipt. Exot., Suppl. 5:29. Amer. Merid.

Tabanus microcerus Wlk. 1848, List, 1:150. Loc.? B. M.

- Tabanus nigripalpis* Macq. 1845, Dipt. Exot., Suppl. 1: 40, pl. 4, figs. 7-8. New Grenada. Coll. Bigot. Placed by Kröber (1931, 1934) in *Catachlorops*, near *rufescens* Fab. A specimen, headless, in Mus. Paris labeled as *rufescens* by Macquart does not disagree with the description, which appears to be based on two different species.
- Pangonia nigronotata* Macq. 1850, Dipt. Exot., Suppl. 4: 27. Mexico. Seen in Mus. Paris by Philip and discussed by him (1954b).
- Tabanus olivaceiventris* Macq. 1847, Dipt. Exot., Suppl. 2: 18. Brazil, Pará. Coll. de Villiers.
- Tabanus opulentus* Wlk. 1848, List, 1: 148. Loc.? B. M.
- Tabanus ornatifrons* Kröber 1930, Dipt. Pat. S. Chile, 5 (2): 153. Chile. B. M. Apparently not returned by Kröber.
- Pangonia planiventris* Macq. 1850, Dipt. Exot., Suppl. 4: 23. Mexico. Placed by Kröber (1934) as a possible synonym of *saussurei* Bell. In Nearctic Coll. at Mus. Paris, where seen by Philip (1954b).
- Tabanus planus* Wlk. 1850, Dipt. Saund., 1: 61. Loc.? B. M.
- Pangonia prasiniventris* Macq. 1846, Dipt. Exot., Suppl. 1: 29. Colombia. Coll. Fairmaire. A specimen ex Coll. Bigot in B. M. is determined by Macquart and can be made neotype if the original fails to turn up.
- Tabanus pubescens* Wlk. 1854, List, 5: 220. Brazil. B. M. A homonym of *T. pubescens* Strom 1768, and Macquart 1847.
- Tabanus pudens* Wlk. 1850, Dipt. Saund., 1: 36. Brazil, Rio de Janeiro. Lutz (1907) = *occidentalis* Wied. Listed as (*Neotabanus*) by Kröber (1934), but he saw no specimens.
- Tabanus redactus* Wlk. 1850, Dipt. Saund., 1: 66. Loc.? B. M.
- Tabanus ruber* Macq. 1845, Dipt. Exot., Suppl. 1: 42. Mexico. Coll. Guerin. A homonym of *T. ruber* Thunb. 1827. Renamed *subruber* by Bellardi, 1859. May be among Nearctic species in Mus. Paris.
- Pangonia rufa* Macq. 1838, Dipt. Exot., 1 (1): 110. Lima (Peru). Coll. Serville. There are specimens determined by Bigot and Kröber in B. M.
- Tabanus scutellatus* Macq. 1839, Dipt. Exot., 1 (2): 186. Loc.? Mus. Paris. Kröber (1934) claims to have seen the type and says it = *macula* Macq., but I was unable to find it and doubt the synonymy. In any case *scutellatus* has six years' priority.
- Tabanus secundus* Wlk. 1848, List, 1: 180. Loc.? B. M.
- Tabanus subsenex* Wlk. 1850, Dipt. Saund., 1: 38. S. America. B. M. Lutz (1907) = *triangulum* Wied.
- Tabanus surinamensis* Macq. 1838, Dipt. Exot., 1 (1): 132. Surinam. Coll. Serville. The description suggests *T. nebulosus* de Geer. Kröber (1934) placed in *Tabanus* with a query.
- Pangonia translucens* Macq. 1845, Dipt. Exot., Suppl. 1: 26. Brazil. Coll. Guerin. The species has long been placed in *Esenbeckia*. (Kröber, 1934; Fairchild, 1942d).
- Tabanus trifarius* Macq. 1838, Dipt. Exot., 1 (1): 144. Chile. Coll. Serville. Genotype of *Archiplatius* End. Kröber (1934) as *Agelanius*.
- Tabanus trifasciatus* Macq. 1834, Hist. Nat. Dipt., 1: 204. Loc.? Coll. Percheron. *T. austeni* var. *trifasciatus* Szil. 1915, appears to be a homonym.
- Tabanus variventris* Macq. 1847, Dipt. Exot., Suppl. 2: 18. Brazil. Coll. Spinola. There is a specimen in Mus. Paris labeled by Macquart as "*T. erythrogaster* Colomb." and also as "*T. variventris* J. Macq. 2e. Suppl. Colombie." The

former appears to be a MS. name. This specimen is a color variant of *hirtitibia* Wlk., but is not the true type of *variventris*, which was from Brazil and probably different.

Tabanus venustus Kröber 1930, Dipt. Pat. S. Chile, 5 (2) : 155. Chile. B. M. Apparently not returned to B. M. after description.

Tabanus viridiflavus Wlk. 1850, Newman's Zoologist, 5, App., p. lxvi. Brazil. B. M. Lutz (1907) = *mexicanus* L. The description indicates *Chlorotabanus inanis* Fab. in the synonymy of which the name has long been placed.

Pangonia xanthopogon Macq. 1838, Dipt. Exot., 1 (2) : 179. Brazil, Goyaz. Mus. Paris. Lutz (1909) regarded a specimen in Mus. Paris labeled *fulvibarbis*, the Latin equivalent of the Greek *xanthopogon*, as probably the type. I did not know of this at the time and did not see the specimen.

It is to be noted that most of the types of Macquart which could not be found in the Paris Museum are species he received from other collectors. Thus, of four species from the Marquis de Spinola, none was found; of eight from the Serville collection, none is in Paris, and one was found in the British Museum. Species described from the collections of de Villiers, Robyns, Guérin, and de Breme, six in all, are all missing from the Paris Museum. The Bigot material and most of the Fairmaire species are in the British Museum save for a few apparently lost. Of the 50 species I have been able to check, described from the Paris Museum collections, only 6 are apparently missing, and these were mainly species without locality which may have been placed elsewhere in the collections.

Dr. C. B. Philip, who has examined a large proportion of the types discussed here, as well as many of Wiedemann's types, has very generously gone over the manuscript of this paper and made numerous suggestions and corrections. He was also fortunate in discovering certain types of Macquart's species in Paris which I did not see, and I append here the information on them he has furnished, as his observations cannot properly be placed with my own.

Pangonia bicolor Macq. 1850. 2 ♀ cotypes in Paris confirm synonymy with *P. semiflava* Wied.

Chrysops frontalis Macq. 1838. 1 ♂ type in Paris with dichoptic eyes and peculiar wing pattern.

Tabanus fulvilateralis Macq. 1838 is the same as the Nearctic *T. (Hybomitra) haemaphorus* Marten 1882, and agrees with a specimen from Alaska in Dr. Philip's collection.

Tabanus scutellatus Macq. 1839. 2 ♀ cotypes in Paris are not the same as *T. macula* Macq. 1845.

In the following list the names are arranged alphabetically. Each name is followed by a condensed citation to its original proposal with the generic name under which it was proposed in parentheses, and the location of the material studied indicated by "B. M." for the British

Museum, "M. P." for the Muséum d'Histoire Naturelle in Paris. Names of which I have seen the types are preceded by an asterisk (*). Where I was able to match the type with a specimen in my possession I have placed an (H) after the location of the type. Some of these specimens are the property of the U. S. National Museum or the Museum of Comparative Zoology at Harvard University, and will be returned to those collections. The remainder are in my collection and will be retained for the time being.

Names which appear to be valid are in **boldface**; all others in *italics*. Synonymy believed to be new is indicated by (N. S.). In the case of confirmation of older synonymy, an attempt has been made to indicate the earliest authority for it, although in some cases this has not been possible. Since I have not examined the types of Wiedemann's species, cases where his names appear to be the earliest valid ones are accepted from the literature.

The supraspecific categories of Neotropical Tabanidae are still in a chaotic condition, though Dr. I. M. Mackerras has in preparation a revision of the whole family, and I have been privileged to see his manuscript. Most of the names here used are in the sense of Kröber's (1934) catalog, the exceptions being the following: *Fidena* includes *Fidena* and *Melpia* of the catalog. *Scaptia* s.s. includes *Osca* and *Caliosca*. *Scaptia* subgenus *Pseudoscione* includes *Listriosca*, *Listrapha*, *Parosca*, *Listraphella*, and probably *Lilaena* of the catalog. *Stenotabanus* includes all the small *Tabanus*-like species with bare subepaulets and at least some of the species placed in *Stypommia* and *Stypommisa* in the catalog. *Aegialomyia* is treated as a subgenus of *Stenotabanus*. *Dasybasis* is used for the species placed in *Agelanius* in the catalog, following Stone (1944), the criterion being bare subepaulets, generally broad frons, and often pilose eyes, the species being mainly Chilean. *Dasychela* End. is used for those species with generally hairy eyes, long antennal tooth, bare subepaulet, and fleshy labella placed in *Di cladocera* in the catalog. The bulk of the species are from Colombia, Ecuador, and Peru. *Di cladocera* is retained for the mainly southern Brazilian forms, which differ in having usually bare eyes and more or less sclerotized labella. *Dichelacera* includes *Catachlorops*, *Amphichlorops*, and *Psalidia* as subgenera. *Tabanus* includes *Allioma* and *Che lommia* of the catalog, and, in fact, all Tabaninae with setose subepaulets except *Leucotabanus*. *Lophotabanus*, *Hybomitra*, *Philipotabanus*, and *Hemichrysops* are retained as subgenera. Future careful work will no doubt modify many of the above categories, but this is not the place for detailed discussion of generic concepts. If the species appears to have been correctly placed generically by the original de-

scriber, I have not added any generic placement. If not, I have added what appears to me the correct generic name in **boldface** type. In the cases where a good modern description or discussion clearly referring to the species exists, I have added the appropriate reference to it.

- **adustus* Wlk. 1850, Dipt. Saund., 1: 34. (*Tabanus*) B. M.(H) = **rubiginipennis* Macq. 1845, Kröber (1934, 1940) as *Dicladocera*.
- **albicans* Macq. 1845, Dipt. Exot., Suppl. 1: 37. (*Tabanus*) B. M.(H). Not Macq. 1833 or 1834. Not **L. canithorax* Fchld. 1941. = *Leucotabanus exaestuans* L. 1767 (N. S.).
- **albidicollis* Macq. 1850, Dipt. Exot., Suppl. 4: 32. (*Tabanus*) B. M.(H) = **T. importunus** Wied., Kröber (1934). Fairchild (1942f).
- **albidocinctus* Big. 1892, 5: 686. (*Tabanus*) B. M. = *Stenotabanus*. Kröber (1934) as *Leucotabanus*.
- **albifasciata* Macq. 1845, Dipt. Exot., Suppl. 1: 28. (*Pangonia*) B. M. = *Scione*. Kröber (1934) has it *albofasciata* in error.
- **albifrons* Macq. 1838, Dipt. Exot., 1(1): 108. (*Pangonia*) M. P.(H) = (*Pseudoscione*). Kröber (1934) as *Lilacina* Borg. Genotype.
- **albipectus* Big. 1892, 5: 611. (*Mycteromyia*) B. M. Kröber (1933b) = *Fidena lingens* Wied.
- **albitarsis* Macq. 1850, Dipt. Exot., Suppl. 4: 36. (*Lepiselaga*) M. P. Kröber (1929d).
- **albithorax* Macq. 1838, Dipt. Exot., 1 (1): 107. (*Pangonia*) M. P. = *Scaptia*. Kröber (1930k, 1934) as *Osca*.
- **alboater* Wlk. 1850, Zoologist, 8, App., p. lxvii. (*Tabanus*) B. M.(H) = **T. atricornis* Big. 1892. = **T. albibarbis** Wied., Kröber (1932b). **T. angustifrons* Macq. 1847, **T. senior* Wlk. 1850, and *Chelommia amazonensis* Barr. 1949, are probably all variants. *Alboater* and *atricornis* agree precisely with each other but differ from *albibarbis* in open first posterior cell and less fumose wings. *Senior* agrees best with *albibarbis* det. Kröb. *Angustifrons* has clear wings and slightly different antennae and palps.
- **albohirtus* Wlk. 1857, Trans. Linn. Soc. London, 17: 338. (*Tabanus*) B. M. = *Dasybasis*. Kröber (1930i, 1934) as *Agelanius*.
- **albomaculatus* Wlk. 1854, List, 5: 207. (*Tabanus*) B. M.(H) = ***T. discifer** Wlk. 1850. Kröber (1931c) as *Gymnochela discifer*; (1934) as *Chelommia discifer*.
- **albomarginata* Kröb. 1930, Zool. Anz., 90 (3-4): 76. (*Spheciogaster*) B. M. Fairchild (1939) as *Acanthocera*.
- **albopicta* Big. 1892, 5: 633. (*Dichelacera*) B. M.(H) = *Catachlorops* *potator* Wied., Lutz (1907) = **Dichelacera marmorata* Big., Lutz (1907).
- **albovarius* Wlk. 1854, List, 5: 206. (*Tabanus*) B. M.(H) = **T. uncinatus* Wlk. 1857 = **Leucotabanus leuconotum* Fchld. 1941 (N.S.).
- **albovittatus* Kröb. 1930, Dipt. Pat. S. Chile, 5, fasc. 2: 146. (*Theriopectes*) B. M. = **Dasybasis scutulatus* Kröb. 1930. (N.S.) Kröber (1934) as *Sciladynus*.
- **alcis* Will. 1896, Trans. Ent. Soc. London, pt. 3, p. 302. (*Tabanus*) B. M. = *Dichelacera*, Bequaert (1940).
- **alene* Towns. 1895, Trans. Amer. Ent. Soc., 22: 59. (*Tabanus*) B. M. = **Stenotabanus parallelus* Wlk., Bequaert (1940).

- **alteripennis* Wlk. 1860, Trans. Ent. Soc. London, 5: 275. (*Tabanus*) B. M.(H) = *T. caliginosus* Bell. 1859, Hine (1925). Fairchild (1953) as (*Philipotabanus*). Philip (1954).
- **altivagus* O. S. 1886, Biol. Cent.-Amer., Dipt., 1: 45. (*Chrysops*) B. M.
- **anabilis* Wlk. 1848, List, 1: 154. (*Tabanus*) B. M. = *T. (Hybomitra) quadripunctatus* Fab. 1805. Kröber (1934).
- **angustifrons* Kröb. 1930, Zool. Anz., 90(3-4): 74. (*Diachlorus*) B. M. = ? *D. ochraceus* Kröb. 1928. Not Macquart 1850. Type appears teneral and may be composite. (N.S.)
- **angustifrons* Macq. 1847, Dipt. Exot., Suppl. 3: 12. (*Tabanus*) B. M.(H) = ? *T. albibarbis* Wied. See remarks under *alboater* Wlk. (N.S.)
- **angustifrons* Towns. 1895, Trans. Amer. Ent. Soc., 22: 59. (*Tabanus*) B. M. = *T. townsendi* Johns., nom. nov. = *T. lucidulus* Beq. 1940 in part. = *T. lucidulus* Fchld. 1951.
- **angustus* Macq. 1838, Dipt. Exot., 1 (1): 136. (*Tabanus*) M. P.(H) = **T. polytaenia* Big. 1892 = ? *T. duplozittatus* Rond. 1868, Brethes (1910).
- **apicalis* Macq. 1847, Dipt. Exot., Suppl. 2: 20. (*Tabanus*) B. M.(H). Two specimens labeled type and paratype, the first bearing a Macquart label. The species was described as headless, but the present type has its own head. The paratype has head glued on. It is possible that Bigot or someone else glued a head of this group onto the true type and switched the label to the more perfect specimen. The type above agrees with "*bigoti* var. B," the paratype with "*bigoti* var. A" of Fairchild (1942). = *T. bigoti* Bell., nom. nov.
- **approximans* Wlk. 1848, List, 1: 198. (*Chrysops*) B. M.(H) = *Diachlorus ferrugatus* Fab. 1805.
- **ataenia* Macq. 1838, Dipt. Exot., 1 (1): 156. (*Diabasis*) M. P. This specimen is probably the one from Pará mentioned in original description. = *Diachlorus curvipes* Fab. 1805, Lutz (1907). Type headless.
- **atricornis* Big. 1892, 5: 683. (*Tabanus*) B. M.(H) = **T. alboater* Wlk. (q. v.) = ? *T. albibarbis* Wied. Not *T. atricornis* Meig. 1838.
- **atrifera* Wlk. 1860, Trans. Ent. Soc. London, 5: 272. (*Pangonia*) B. M. = *Pangonia haustellata* (Fab.) 1781. Palearctic. Philip (1954).
- attenuatus* Wlk. 1848, List, 1: 159. (*Tabanus*) B. M. Probably Oriental; does not appear to be Neotropical, and may not be the true type.
- **aureopygia* Kröb. 1931, Zool. Anz., 95: 24. (*Fidena*) B. M.
- **auribarbis* Macq. 1847, Dipt. Exot., Suppl. 3: 12. (*Tabanus*) B. M.(H) = **Dasychela macula* Macq. 1845. Kröber (1934, 1940) as *Di cladocera macula*.
- **aurimaculata* Macq. 1838, Dipt. Exot., 1(1): 109. (*Pangonia*) M. P.(H) = *Fidena*, Kröber (1934).
- **auripes* Ric. 1900, Ann. Mag. Nat. Hist., ser. 7, 5: 176. (*Erephrosis*) B. M.(H) = *Fidena*, Kröber (1934).
- **aurisquamatus* Big. 1892, 5: 665. (*Atylotus*) B. M. = *Atylotus fulvus* Meig. Palearctic. (N.S.) Lutz (1907) = *T. unicolor* Wied.
- **auroguttata* Kröb. 1930, Zool. Anz., 90(3-4): 71. (*Chrysops*) B. M. Bequaert (1944). A distinct species from *C. auroguttata pallidifemorata* Kröb.
- **aurora* Macq. 1838, Dipt. Exot., 1(1): 142. (*Tabanus*) M. P. Not *T. aurora* of Lutz (1914, 1918), Bequaert (1926), or Kröber (1929c). Near *T. ferreus* Wlk. 1848 and *T. impressus* Wied. 1828.
- **austeni* Kröb. 1930, Zool. Anz., 86(11-12): 294. (*Tabanus*) B. M. Not *Tabanus* (*Ochrops*) *austeni* Szil. (1915, Ent. Mitt. Berlin, 4: 100). For *Tabanus*

- (*Phacotabanus*) *austeni* Kröb. I hereby propose the name *Tabanus sannio*, nom. nov.
- **badia* Wlk. 1848, List, 1: 132. (*Pangonia*) B. M. = *Fidena venosa* Wied. 1828, Kröber (1930g) as *Sackenimyia venosa*; (1934) as *Melpia*.
- **badia* Kröb. 1931, Rev. Ent., 1 (4): 402. (*Dicladocera*) B. M.(H) = *Dasychela*. Fairchild (1940b).
- **bahiana* Big. 1892, 5: 612. (*Pangonia*) B. M. = **Pangonia flavescens* Ric. 1900a. = *Esenbeckia vulpes* Wied. 1828, Kröber (1932a).
- **basalis* Wlk. 1848, List, 1: 133. (*Pangonia*) B. M.(H) = *Fidena basilaris* Wied. 1828. Lutz (1909) as *Phaeoneura basilaris* Wied. Kröber (1933b) as *F. basilaris* Wied. Not *Pangonia basalis* Macq. 1847. Palearctic. Not listed by Kröber (1934).
- **basi-rufus* Wlk. 1850, Dipt. Saund., 1: 32. (*Tabanus*) B. M.(H) = *Dasychela*, Bequaert and Renjifo (1946). Kröber (1940) as *Dicladocera*.
- **basi-vitta* Wlk. 1850, Zoologist, 8, App., p. lxviii. (*Tabanus*) B. M.(H) = **T. viduus* Wlk. 1850. = **T. bitinctus* Wlk. 1857. = ? *T. marginenevris* Macq. 1855. Type not found, but specimens det. Bigot in B. M. agree with *basi-vitta*. (N.S.)
- **bicolor* Big. 1892, Wien. Ent. Zeitg., 11: 162. (*Bolbodimyia*) B. M.(H). Stone (1954).
- **bicolor* Big. 1892, 5: 636. (*Stibasoma*) B. M. = *Stibasoma triste* (Wied.) 1828. Lutz (1915). Kröber (1934). Not *Tabanus tristis* Fab. 1798.
- **bifascies* Wlk. 1848, List, 1: 191. (*Dichelacera*) B. M.(H). Barretto (1949b) as *Rhamphis* End.
- **bifenestratus* O. S. 1886, Biol. Centr.-Amer., Dipt., 1: 52. (*Tabanus*) B. M. Philip (1952).
- **bipartitus* Wlk. 1848, List, 1: 158. (*Tabanus*) B. M.(H) = **T. (Lophotabanus) oculus* Wlk. 1848, p. 157. Kröber (1934). Fairchild (1942b) as *Bellardia*.
- **bitinctus* Wlk. 1857, Trans. Ent. Soc. London, 4 (5): 123. (*Tabanus*) B. M.(H) = **T. basivitta* Wlk. 1850. (N.S.)
- **brasiliensis* Ric. 1901, Ann. Mag. Nat. Hist., ser. 7, 8: 314. (*Chrysops*) B. M.(H) = **Chrysops incisa* Macq. (q. v.). (N.S.)
- **brunnipes* Kröb. 1929, Encycl. Ent., Dipt. 5: 116. (*Stenotabanus*) B. M. = *Stenotabanus*, with bare subepaulets. The specimen is a paratype.
- **callicera* Big. 1892, 5: 686. (*Tabanus*) B. M. Appears related to *Stenotabanus pequeniensis* Fchld. 1942a. Subepaulets with sparse macrotrichiae. Lutz (1907) = ? *rubrithorax* Macq. 1838.
- **callosus* Macq. 1848, Dipt. Exot., Suppl. 3: 11. (*Tabanus*) B. M.(H) = ? *T. trivittatus* Fab. Not *T. callosus* Fairchild 1942c. Type lacks antennae and palps and further series may show intergrading with other named forms, as in *lincola* complex. Philip (1954b).
- **campechianus* Towns. 1897, Canadian Ent., 29: 197. (*Tabanus*) B. M. A *Tabanus* nearest *yucatanus* Towns. but quite distinct.
- **carbo* Macq. 1850, Dipt. Exot., Suppl. 4: 33. (*Tabanus*) B. M. and M. P.(H) = *Veprius presbiter* Rond. 1863. Kröber (1929a) as *Stypommia*. The types have hind tibial spurs, bare subepaulets and subcosta and well-developed ocelli, so that *carbo* will replace Rondani's specific name. (N.S.)
- **castanea* Big. 1892, 5: 633. (*Dichelacera*) B. M.(H) = *Dicladocera*. Kröber (1931c) as var. of *Gymnochela satanica* Big.; (1934) as syn. of *Chelommia*

- satanica* Big. Not *Chelommia castanea* Barr. 1949a. Subepaulets bare. Type agrees quite well with a specimen det. Fairchild as *Di cladocera unicolor* Lutz from the description. Barretto (1948) as syn. of *Amphichlorops satanica* Big. = ? *Amphichlorops ferruginea* Barr. 1948.
- **castanea* Surc. 1919, Mes. Arc. Mérid. Équat. Amér. du Sud, 10: 222. (*Erc-phopsis*) M. P. = *Fidena castaneiventris* Kröb. 1934, nom. nov. Not *Fidena castanea* (Perty) 1830.
- **caustica* O. S. 1886, Biol. Centr.-Amer., Dipt., 1: 44. (*Pangonia*) B. M. = *Esenbeckia wiedemanni* Bell., Kröber (1934). Philip (1954a) as a distinct species.
- **chilensis* Macq. 1838, Dipt. Exot., 1(1): 145. (*Tabanus*) M. P.(H) = *Dasybasis*. Kröber (1934) as *Agelanius*.
- **chionostigma* O. S. 1886, Biol. Centr.-Amer., Dipt., 1: 54. (*Tabanus*) B. M. = *Stibasoma*, Fairchild (1940b). Labels on type do not agree with original description.
- **cinerascens* Big. 1892, 5: 610. (*Mycteromyia*) B. M. Kröber (1930f).
- **cingulifer* Wlk. 1857, Trans. Ent. Soc. London, 4(5): 123. (*Tabanus*) B. M. = *Leucotabanus exaestuans* Linn. 1767.
- **claripennis* Big. 1892, 5: 675. (*Atylotus*) B. M.(H) = *Tabanus hookeri* Knab 1915 (N.S.). Original locality given as Australia. Bequaert (1940).
- **clausus* Macq. 1847, Dipt. Exot., Suppl. 2: 17. (*Tabanus*) B. M.(H) = *Tabanus fuscus* Wied. 1828. Lutz (1907); Kröber (1934) as syn. of *Chelotabanus fuscus* Wied.
- **colombensis* Macq. 1846, Dipt. Exot., Suppl. 1: 37. (*Tabanus*) B. M.(H) = *T. amplifrons* Kröb., Fairchild (1942c). = **T. fur* Will. 1901. Kröber (1933a) as syn. of *T. occidentalis* Linn. (N.S.)
- **columbiensis* Kröb. 1930, Mitt. Mus. Hamburg, 44: 177. (*Melpia*) B. M.(H) = *Fidena*, Kröber (1934); Fairchild (1951a).
- **commixtus* Wlk. 1860, Trans. Ent. Soc. London, 5: 273. (*Tabanus*) B. M.(H) = **Tabanus maya* Bequaert 1932. Fairchild (1942c). Kröber (1934) as syn. of *T. lincola* Fab. (N.S.)
- **communis* Kröb. 1931, Stett. Ent. Zeitg., 92: 282. (*Agelanius*) B. M. = **T. frequens* Kröb. 1934, nom. nov. Not *T. communis* Kröb. 1930. = *Dasybasis*, with bare subepaulets.
- **compactus* Wlk. 1854, List, 5, Suppl. 1: 222. (*Tabanus*) B. M.(H) = *Stibasoma fulvohirtum* Wied. 1828, Osten Sacken (1886).
- **comprehensa* Wlk. 1850, Dipt. Saund., 1: 11. (*Pangonia*) B. M.(H) = *Elaphella cervus* Wied. 1828, Ricardo (1904).
- **confinis* Wlk. 1848, List, 1: 160. (*Tabanus*) B. M. = ? *T. aurilineatus* Sch.-Stekh. 1926, Oriental. Not *T. confinis* Zett. 1840. Lutz (1907) = *T. taeniotes* Wied. Kröber (1933a) as (*Neotabanus*). Not Neotropical, in my opinion.
- **confligens* Wlk. 1854, List, 5, Suppl. 1: 326. (*Tabanus*) B. M.(H). Nom. nov. pro **T. tenens* Wlk. 1850, Zoologist, 8, App., p. lxxv, and 1854, List, 5, Suppl. 1: 123. Not *tenens* Wlk. 1850, Dipt. Saund., 1: 49. E. India. = *T. cinerarius* Wied. 1828, Kröber (1931c, 1934) as *Chelommia* or *Gymnochela*.
- **conica* Big. 1857, Ann. Ent. Soc. France, ser. 3, 5: 278. (*Pangonia*) B. M.(H) = *Mycteromyia* Philippi, genotype. Kröber (1930f).
- **consequa* Wlk. 1850, Zoologist, 8, App., p. cxxi. (*Tabanus*) B. M.(H) = ? *T. lineola* var. *carneus* Bell., Fairchild (1942c). = **T. globulicallus* Kröb. 1931. = ? *T. dorsiger* var. *pallidefemorata* Kröb. 1929. = ? *T. ochro-*

- philus* Lutz 1914. This is the small pale form of *lineola* var. *carneus* (N.S.). Until the relationships in this group can be thoroughly worked out it seems better to retain *dorsovittatus* Macq. (q.v.) as separate.
- **convergens* Wlk. 1848, List, 1: 198. (*Chrysops*) B. M. = *Diachlorus ferrugatus* Fab., Ricardo (1904).
- **cornuta* Wlk. 1857, Trans. Linn. Soc. London, 17(3): 337. (*Pangonia*) B. M.(H) = *Rhabdotylus planiventris* (Wied.) 1828, Lutz (1907). Kröber (1934) as *Amphichlorops*.
- **corone* O. S. 1886, Biol. Centr.-Amer., Dipt., 1: 51. (*Tabanus*) B. M.(H).
- **cribellum* O. S. 1886, Biol. Centr.-Amer., Dipt., 1: 52. (*Tabanus*) B. M. = *Stenotabanus*, Stone (1938); Philip (1950).
- **cyaneum* Wlk. 1848, List, 1: 208. (*Hadrus*) B. M. = *Selasoma tibiale* Fab., Ricardo (1904).
- **depressa* Macq. 1837, Ann. Soc. Ent. France, 6: 429; 1838, Dipt. Exot., 1: 111. (*Pangonia*) B. M. and M. P.(H) = *Scaptia lata* Guerin 1830. Walker (1850), genotype of *Oscia*. Rondani (1863), genotype of *Diatomineura*.
- **derivatus* Wlk. 1848, List, 1: 151. (*Tabanus*) B. M. = ? (*Lophotabanus*). Type headless, unrecognizable, a male. Name should not be used for specimens, in my opinion. Described from North America. Not listed by Kröber (1934).
- **desertus* Wlk. 1850, Zoologist, 8, App., p. lxix. (*Tabanus*) B. M.(H) = **T. nuntius* Wlk. 1854. = **T. univittatus* Macq. 1855. = *T. sallei* Bell. 1859. = *T. angustivitta*, Fchld. 1942. = **T. (Agelanius) ruficolor* Kröb. 1934. = **T. discifer* Big. 1892. = ? *T. dorsiger* var. *angustivitta* Kröb. 1929. Bodkin and Cleare (1916) (N.S.).
- **detersus* Wlk. 1850, Dipt. Saund., 1: 31. (*Tabanus*) B. M. = *Stenotabanus* near *pompholyx* Fchld. Kröber (1930c) as *Macrocornus*.
- **discifer* Wlk. 1850, Dipt. Saund., 1: 35. (*Tabanus*) B. M.(H) = **T. albo-maculatus* Wlk. 1854. Kröber (1931c) as *Gymnochela*; (1934) as *Chelommia*.
- **discifer* Big. 1892, 5: 684. (*Tabanus*) B. M.(H) = **T. desertus* Wlk. 1850. Not **T. discifer* Wlk. 1850. (N.S.)
- **diversipennis* Wlk. 1848, List, 1: 165. (*Tabanus*) B. M.(H) = **Esenbeckia fascipennis* Macq. 1838, Kröber (1934).
- **diversipes* Macq. 1848, Dipt. Exot., Suppl. 3: 13. (*Diabasis*) B. M. = *Diachlorus bicinctus* Fab. 1805. Lutz (1913); Kröber (1928b).
- **dives* Wlk. 1848, List, 1: 166. (*Tabanus*) B. M.(H) = **Stibasoma flaviventris* Macq. 1847, Lutz (1915). Kröber (1934) as var. of *fulvohirtum* Wied.
- **dominicanus* Kröb. 1931, Stett. Ent. Zeitg., 92: 301. (*Tabanus*) B. M. = (*Lophotabanus*) Bequaert (1940).
- **dorsoguttata* Macq. 1850, Dipt. Exot., Suppl. 4: 24. (*Pangonia*) M. P. = *Scaptia (Pseudoscione)*. Kröber (1930k) as *Parosca*; (1934) as *Listrapha*.
- **dorsovittatus* Macq. 1855, Dipt. Exot., Suppl. 5: 30. (*Tabanus*) B. M.(H). = *T. lineola* var. *carneus* Bell., Fairchild 1942. Lutz (1907) = ? *trilineatus* Latr. Kröber (1933a) suggests a var. of *carneus*. Type in poor shape; agrees with pale specimens of var. *carneus* from Pernambuco, Brazil. (N.S.) See under *consequa* Wlk.
- **ebrius* O. S. 1886, Biol. Centr.-Amer., Dipt., 1: 49. (*Tabanus*) B. M.(H) = (*Philipotabanus*) subgenotype. Fairchild (1942f).

- **edwardsi* Kröb. 1930, Dipt. Pat. S. Chile, 5(2): 131. (*Mycteromyia*) B. M. = **Mycteromyia hirtipalpis* (Big.) 1892. (N.S.) Hack (1953).
- **elongatus* Macq. 1845, Dipt. Exot., Suppl. 1: 38. (*Tabanus*) B. M.(H) = *Dichelacera* (*Psallidia*) *vespertina* Bequaert and Renjifo 1946, nom. nov. Not *T. elongatus* Wied. 1828. Kröber (1934) as *Rhamphidommia*. Barretto (1948) as *Amphichlorops*.
- enderleini* Kröb. 1931, Zool. Anz., 94(9-10): 252. (*Esenbeckia*) B. M. The holotype ♂ is in Berlin. The specimens in B. M. det. Kröber, 1 ♂ and 2 ♀, do not agree with Kröber's statements as to sex and locality, are probably not the same species (see Lutz and Castro 1935) and are not true types.
- **equatoriensis* Surc. 1920, Mes. Arc. Mérid. Équat. Amér. du Sud, 10: 219. (*Scione*) M. P.(H). Kröber (1930j).
- **erebus* O. S. 1886, Biol. Centr.-Amer., Dipt., 1: 50. (*Tabanus*) B. M.(H) = *Astigmatophthalmus satanus* Kröb. 1931, Stone (1938). Kröber (1934) as syn. of *T. alteripennis* Wlk. Fairchild (1942f) as *Tabanus*.
- **eriomera* Macq. 1838, Dipt. Exot., 1(1): 109. (*Pangonia*) M. P. = **Fidena**. Lutz (1909) as *Epipsila*. Structurally close to *F. rhinophora* Bell.
- **erythraeus* Big. 1892, 5: 687. (*Tabanus*) B. M.(H) = **T. impressus** Wied. 1828. (N.S.) Not *Atylotus erythraeus* Big. 1892, 5: 661. Kröber (1934) as syn. of *T. monochroma* Wied.
- **erythrocephalus* Big. 1892, 5: 668. (*Atylotus*) B. M.(H) = **Bolbodimyia**, Kröber (1930h). Stone (1954).
- **erythronotata* Big. 1892, 5: 612. (*Mycteromyia*) B. M.(H) = **Fidena**. Lutz (1909) as *Bombylopsis*. Kröber (1934) as *Melpia*.
- **eutaeniatus* Big. 1892, 5: 664. (*Atylotus*) B. M.(H) = ? **Tabanus triangulum** Wied., Fairchild (1942c). Type pale and denuded. Does not wholly agree with description. (N.S.) Lutz (1907) suggests syn. of *T. ditaenia* Wied., a species from unknown locality.
- **excelsus* Surc. 1919, Mes. Arc. Mérid. Équat. Amér. du Sud, 10: 228. (*Tabanus*) M. P. Not *T. excelsus* Ricardo (1913, Ann. Mag. Nat. Hist. (8) 11: 543, India). The type bears the MS. name *excelsior* Surc., indicating an intention on Surcouf's part to change his homonym; *excelsior* is hereby proposed for *excelsus* Surc. 1919, not Ricardo 1913. Kröber (1934) as ? *Stypommia*. Bequaert and Renjifo (1946) as *Agelanius*. = *Dasybasis*.
- **excursus* Wlk. 1850, Dipt. Saund., 1: 12. (*Pangonia*) B. M. = ? (**Pseudoscione**) *molesta* Wied. 1828. Near *seminigra* Ric. Enderlein (1925) as *Melpia* genotype. Not *Melpia* Wlk. Kröber (1930k) as syn. of *Parosca molesta* Wied.; (1934) as *Listrapha molesta* Wied.
- **fallax* Macq. 1847, Dipt. Exot., Suppl. 2: 20. (*Tabanus*) B. M. Not *T. fallax* Macq. 1845, Africa. Kröber (1932b, 1934) as *Chelotabanus fallax*. Type very dirty. Apparently related to *bigoti*, but I could not match among my material. A new name may be needed when this group is straightened out.
- **fasciata* Macq. 1834, Hist. Nat. Ins. Dipt., 1: 194; 1838, Dipt. Exot., 1(1): 107. (*Pangonia*) M. P. Not *P. fasciata* Latr. 1811, Egypt. Lutz (1907) as syn. of *Esenbeckia esenbeckii* Wied. 1830. There are 10 ♀ in Mus. Paris, apparently conspecific. Related to *insignis* Kröb., *filipalpis* Will., *clari* Lutz, and *nigricorpus* Lutz.
- **fasciata* Wlk. 1850, Dipt. Saund., 1: 68. (*Dichelacera*) B. M.(H) = **Dichelacera analis* Hine 1920. = *D. costaricensis* Kröb. 1931, Fairchild (1940b).

- Osten Sacken (1886), Ricardo (1904), Kröber (1934) as syn. of *D. cervicornis* Fab. (N.S.)
- **fascipennis* Macq. 1845, Dipt. Exot., Suppl. 1:35. (*Tabanus*) B. M.(H) = (*Philipotabanus*) Fairchild (1942f).
- **fascipennis* Macq. 1838, Dipt. Exot., 1(1):110. (*Pangonia*) M. P.(H) = **Esenbeckia diversipennis* Wlk. 1848, Kröber (1934).
- **fascipennis* Kröb. 1930, Zool. Anz., 88(9-10):237. (*Hemichrysops*). The type lacks hind legs, but another specimen (Carillo, Costa Rica) in B. M. retains them and shows no spurs. Subepaulet sparsely setose. The genus is tabanine not pangoniine and close to *Philipotabanus*, from which it may be separated by more protuberant face and sunken frons. The specific name will fall as a homonym of *Tabanus fascipennis* Macq. 1845. The new specific name of *vecordis* is hereby proposed and the species may be known as **Tabanus** (*Hemichrysops*) *vecordis*, nom. nov.
- **fenestratus* Macq. 1838, Dipt. Exot., 1(1):139. (*Tabanus*) M. P.(H) = **Pachyschelomyia notopleuralis** Barr. 1950. Brethes (1910) and Kröber (1934) as *Sibasoma*. The species is an aberrant one, resembling the African *Ancala africana* in inflated tibiae and general fascies, but with bare subepaulets and sclerotized labella. It seems closest to *Phacotabanus* Lutz among Neotropical species. Barretto's name seems tenable. Not *T. fenestratus* Fab. 1794. (N.S.)
- **fenestrata* Macq. 1845, Dipt. Exot., Suppl. 1:26. (*Pangonia*) B. M. = (*Pseudoscione*). Lutz (1909) as *Diatomineura*. Kröber (1930k) as *Parosca*; (1934) as *Listrapha*. Very close to *seminigra* Ric. and *longipennis* Ric.
- **ferreus* Wlk. 1848, List, 1:151. (*Tabanus*) B. M.(H). Lutz (1907) = ? ? *D. rufipennis* Macq. Kröber (1932b) as *Chelotabanus ferreus*. Very close to *T. impressus* Wied. 1828, but darker.
- **ferrifer* Wlk. 1850, Dipt. Saund., 1:30. (*Tabanus*) B. M. (H) = **Tabanus nebulosus** de Geer, Philip (1952). Fairchild (1942f).
- **ferruginea* Macq. 1839, Dipt. Exot., 1(2):295. (*Pangonia*) M. P.(H) = **Esenbeckia illota* Will., Fairchild (1942d). Not *Tanyglossa ferruginea* Latr. 1809. The type is like the form treated by Fairchild (1942d) as *E. i. enderleini* Kröb. but with slightly more slender palpi.
- **ferruginosus* Wlk. 1850, Dipt. Saund., 1:40. (*Tabanus*) B. M. = **Stenotabanus**. Kröber (1930c) as *Macrocornus*. Subepaulet bare. Near **jaculator* Fchld. and *fulviventris* Macq.
- **filiolus* Will. 1901, Biol. Centr.-Amer., Dipt., 1, Suppl. :261. (*Tabanus*) B. M.(H) = ***Tabanus haemagogus** Will., Hine (1925). Bequaert (1931).
- **flavescens* Ric. 1900, Ann. Mag. Nat. Hist., ser. 7, 5:174. (*Pangonia*) B. M. = **Esenbeckia vulpes** Wied., Lutz (1907); Kröber (1932a).
- **flavinetum* Kröb. 1934, Rev. Ent., 4(3):309. (*Tabanus*) B. M.(H). Nom. nov. pro *T. nigriflavus* Kröb. (1931, Konowia, 10(4):292) = **Leucotabanus**, Fairchild (1941). Not *T. nigriflavus* Kröb. 1930.
- **flavipennis* Macq. 1850, Dipt. Exot., Suppl. 4:35. (*Diabasis*) B. M. The type is in poor shape, subepaulets with a few macrotrichiae, antennae *Tabanus*-like. Said to be from Philippine Islands. The species is a *Tabanus*, in my opinion, and the name should not be added to the Neotropical fauna without further evidence. It will preoccupy *T. flavipennis* Ric. 1914, from the Moluccas.

- ***flaviventris** Macq. 1847, Dipt. Exot., Suppl. 3: 90. (*Tabanus*) B. M.(H) = **Stibasoma**, Lutz (1915) with *dives* Wlk. 1848, as syn. = **T. dives* Wlk. 1848; = *St. euglossa* Lutz 1915 (fig. only, no description); = **St. stilbium* Fchld. 1953; = *St. mallophoroides*, J. Beq. 1944, not Walker 1857; = ? *St. sulfurotaeniatum* Kröb. 1921 (N.S.). Trinidad specimens lack complete yellow hind marginal bands on all tergites except the second, but differ in no other way from the type and specimens from South and Central America.
- ***flavohirta** Ric. 1902, Ann. Mag. Nat. Hist., ser. 7, 9: 437. (*Scione*) B. M. The specimen in B. M. is an allotype. The type ♂ was returned to Budapest.
- ***fulva** Ric. 1902, Ann. Mag. Nat. Hist., ser. 7, 9: 435. (*Scione*) B. M. The specimen is a paratype; others returned to Budapest. Kröber (1930j).
- ***fulvilateralis** Macq. 1838, Dipt. Exot., 1(1): 137. (*Tabanus*) M. P. = (**Hymbomitra**). Eyes pilose, vertical tubercle and setose subepaulets. Possibly Palearctic or Nearctic; probably not from Cayenne, as stated.
- ***fulvitibialis** Ric. 1900, Ann. Mag. Nat. Hist., ser. 7, 5: 177. (*Erephrosis*) B. M. = **Fidena**, Kröber (1934). Near *rhinophora* Bell. but with longer palpi and face, more slender antennae and wholly dark abdomen.
- ***fulviventris** Macq. 1845, Dipt. Exot., Suppl. 1: 36. (*Tabanus*) B. M.(H). Kröber (1930a) as *Stypommisa*. Subepaulets setose.
- ***fulvosericca** Kröb. 1931, Zool. Anz., 95(1-2): 26. (*Fidena*) B. M.(H) = ***Scione rufescens** (Ric.) 1900; = **Scione aureopygia* Fchld. 1942. (N.S.)
- ***fumifera** Wlk. 1854, List, 5, Suppl. 1: 323. (*Pangonia*) B. M. = **Fidena**, Kröber (1933b). **F. loricornis* Kröb. 1931 and *Erephopsis pseudoaurimaculata* Lutz 1909 are separable with difficulty, and all three species are from the Amazon basin.
- ***fur** Will. 1901, Biol. Centr.-Amer., Dipt., 1, Suppl. : 261. (*Tabanus*) B. M.(H) = ***Tabanus colombensis** Macq. Not *T. fur* Will. 1887 (N.S.).
- ***furcata** Big. 1892, 5: 631. (*Bellardia*) B. M.(H) = ***Dichelacera** (**Psalidia**) **fulminea** Hine. Not *D. (Ps.) furcata* (Wied.) 1828. This is the light form of the species named *ocellata* by Enderlein and *festiva* by Hine. See Fairchild (1951a) (N.S.). Not listed by Kröber (1934).
- ***furunculus** Will. 1901, Biol. Centr.-Amer., Dipt., 1, Suppl. : 260. (*Tabanus*) B. M.(H).
- ***fuscicrura** Big. 1892, 5: 662. (*Atylotus*) B. M.(H) = **Tabanus subruber** Bell., Philip (1952).
- ***fuscinevris** Macq. 1839, Dipt. Exot., 1(2): 184. (*Tabanus*) M. P.(H) = **Catachlorops intereuns* (Wlk.) 1856 (N.S.). Lutz (1907) noted it was probably Neotropical. Kröber (1934) not listed. Oldroyd (1954).
- ***fuscipennis** Macq. 1847, Dipt. Exot., Suppl. 2: 14. (*Dichelacera*) B. M.(H) = *Catachlorops psoloptera* (Wied.) 1828. Bequaert (1924) genotype of *Catachlorops*. Kröber (1934, 1939); Barretto (1946). Type agrees with specimen of *psoloptera* det. Barretto.
- ***fuscipennis** Macq. 1838, Dipt. Exot., 1(1): 156. (*Diabasis*) M. P. = **Leptapha fumata** (Wied.) 1821 (N.S.).
- ***fuscofasciatus** Macq. 1838, Dipt. Exot., 1(1): 140. (*Tabanus*) M. P.(H) = ***Tabanus hilarii** Macq. 1839.
- ***fuscus** Ric. 1902, Ann. Mag. Nat. Hist., ser. 7, 9: 431. (*Erephrosis*) B. M. Lutz (1907) and Kröber (1933a) as syn. of *Fidena winthemi* Wied. Differs from *winthemi* in B. M. in broader frons, stouter antennae, wholly pollinose clypeus, darker legs and white-haired pleura. Close also to *obscuripes* Kröb.

but differs in broader palps, frons, and antennae, and in abdominal coloring, which is as in *winthemi*. Specimen in B. M. a cotype; the other was in Budapest.

- **fusiformis* Wlk. 1850, Dipt. Saund., 1:19. (*Pangonia*) B. M.(H) = *Esenbeckia translucens* Macq., Hine (1920, 1925); Kröber (1934).
- **globulicallosus* Kröb. 1931, Stett. Ent. Zeitg., 92:302. (*Tabanus*) B. M.(H) = **Tabanus lineola* var. *consequa* Wlk. 1850. = *T. lineola* var. *carneus* Bell. small form (N.S.).
- **grandis* Ric. 1904, Ann. Mag. Nat. Hist., ser. 7, 14:371. (*Dichelacera*) B. M.(H). Kröber (1934).
- **guiterasi* Brunetti 1922, Bull. Ent. Res., 13:401. (*Chrysops*) B. M.(H) = *Chrysops flavida* Wied. 1821, Bequaert (1940). The original description states a ♂ in B. M., a ♀ in Berlin, but the specimen now at B. M. is a ♀ and there is now no ♂ in B. M.
- **guyanensis* Macq. 1845, Dipt. Exot., Suppl. 1:41. (*Tabanus*) B. M.(H) = ? *Tabanus flavibarbis* Macq., Dipt. Exot., Suppl. 1:41. = *T. flavibarbis* of Kröber (1929c, 1930h) and Bequaert (1926). The type of *flavibarbis* could not be found. The description of *guyanensis* precedes on the same page (N.S.).
- **haemagogus* Will. 1901, Biol. Centr.-Amer., Dipt., 1, Suppl. :261. (*Tabanus*) B. M.(H). Bequaert (1931) with **filiolus* Will. as syn.
- **halteratus* Kröb. 1931, Ann. Mus. Hung., 27:344. (*Catachlorops*) B. M. Very close structurally to *C. d'almeidai* Pech. but darker, more brownish facial pollinosity, brown callus and not strongly bicolored fore tibiae. Specimens in B. M. from Br. Guiana det. *luctuosa* by Kröber are the same, but **luctuosa* Macq. is a different species. See Barretto (1946).
- **hemiptera* Surc. 1912, Bull. Mus. Hist. Nat. Paris, pp. 61-63. (*Stibasoma*) M. P. The specimen is ex coll. Bigot labeled "nov. Holl." The head is glued on and may not belong. Labella fleshy, hence not a *Stibasoma*. I believe near *riveti* Surc., *macula* Macq., and *minos* Schin., and will go in *Dasychela*. I doubt its being Australian. Not listed by Kröber (1934).
- **hilarii* Macq. 1839, Dipt. Exot., 1(2):185. (*Tabanus*) M. P.(H) = **T. fuscofasciatus* Macq. 1838/ = ? *T. acer* Brethes 1910. (N.S.)
- **hinnulus* Wlk. 1850, Zoologist, 8, App., p. cxxii. (*Dichelacera*) B. M.(H). = **Dichelacera marginata* Macq. 1847, Ricardo (1904). Kröber (1934) as syn. of *marginata* Macq.
- **hirtipalpus* Big. 1892, 5:619. (*Diatomineura*) B. M.(H) = *Mycteromyia* = **Mycteromyia edwardsi* Kröb. 1930. Kröber (1930f) erected the genus *Caenopangonia* for this species on the basis of supposedly hairy eyes. The type, however, has bare eyes. (N.S.)
- **hirtitibia* Wlk. 1850, Dipt. Saund., 1:33. (*Tabanus*) B. M.(H) = ? *Tabanus cinnamomeus* Schin. 1868. = *Chelommia fibulata* End. 1924. *Alliomma* Borgm. is based on another species of the same group. Bequaert and Renjifo (1946). (N.S.)
- **illota* Will. 1901, Biol. Centr.-Amer., Dipt., 1, Suppl. :254. (*Pangonia*) B. M.(H) = **Esenbeckia ferruginea* (Macq.) Fairchild 1942. Philip (1954a).
- **immaculata* Macq. 1838, Dipt. Exot., 1(1):115. (*Dichelacera*) M. P.(H). = *Amphichlorops angustifrons* Kröb. 1932 = ? *Amphichlorops ferruginea* Barr. 1948. Lutz and Neiva (1914), Kröber (1934), and Barretto (1946)

treat as *Catachlorops*. Specimen in B. M. det. *immaculata* by Kröber agrees with type of **Catachlorops fuscipennis* Macq. The type of *immaculata* is very close to *flavus* Wied. and *vespertina* Beq. and will go into *Amphichlorops*. (N.S.)

**immaculata* Kröb. 1930, Stett. Ent. Zeitg., 91(2): 148. (*Rhinotriclista*) B. M. = *Scione*, Kröber (1934).

**imponens* Wlk. 1857, Trans. Ent. Soc. London, 4: 122. (*Tabanus*) B. M.(H) = *Tabanus olivaceiventris* Macq. 1847 (N.S.) = **Atylotus pulverulentus* Big. 1892. Kröber (1929a) as (*Lophotabanus*) with *pulverulentus* as syn. Bequaert (1926).

**importunus* Macq. 1847, Dipt. Exot., Suppl. 2: 18. (*Tabanus*) B. M. = (*Neotabanus*), Kröber 1933. Not *T. importunus* Wied. 1828. Type very dirty and denuded, apparently a member of *lineola* complex.

**incertus* Macq. 1838, Dipt. Exot., 1(1): 151. (*Tabanus*) M. P.(H) = *Tabanus nebulosus* de Geer 1776 = **T. ferriifer* Wlk. 1850. Not *T. palpalis* var. *incertus* Szil. 1926, East Indies. Blanchard's (1852) reference of specimens from Chile repeated by Kröber (1934) is certainly an error. (N.S.)

**incipiens* Wlk. 1860, Trans. Ent. Soc. London, 5: 275. (*Tabanus*) B. M. = *Stenotabanus*, Kröber (1930h, 1934). Type headless, subepaulets bare. Near *St. maculifrons* Hine, but probably now indeterminable with any certainty.

**incisa* Macq. 1845, Dipt. Exot., Suppl. 1: 177. (*Chrysops*) B. M.(H) = **Chrysops brasiliensis* Ric. 1901 = *C. fulviceps*, Kröber 1925, Bequaert 1940. = ? *C. fulviceps* Wlk. 1845. = *C. aurofasciata* Kröb. 1926. (N.S.) Not *C. fulviceps* Lutz 1909. Not *C. incisa* Fairchild 1942. There are 3 ♀ cotypes; the one bearing Macquart's hand label has been selected and labeled as lectotype. The others are different species.

**incisuralis* Macq. 1847, Dipt. Exot., Suppl. 2: 12. (*Pangonia*) B. M. = ? *Fidena opaca* (Brethes) 1910 = *Fidena albibarba* End. 1925, p. 293, not *Melpia auribarba* var. *albibarba* End. 1925, p. 276 = *Fidena abominata* Philip 1941 = ?? *Tanyglossa hirsuta* Thunberg (1827, Nova Acta R. Soc. Sci. Upsala, 9: 67, Brasilia). Not *Pangonia incisuralis* Say 1823. Enderlein (1925) as syn. of *hirsuta* Thunb. and says *incisuralis* Lutz (1909) = *albibarba* End. Kröber (1933b, 1934) lists as a valid species of *Fidena* and saw type. Castro (1945) identifies *incisuralis* of Lutz (1909) with *longipalpis* End. 1925. All specimens seen by Lutz, Enderlein, Brethes, Castro, and myself are from southern Brazil and Argentina. The eyes are practically bare and frons with a pair of low bosses at base. The correct name for this species must await examination of Brethes and Thunberg's types, if still in existence.

incompleta Macq. 1845, Dipt. Exot., Suppl. 1: 27. ♂ ♀; 1850, op. cit. Suppl. 4: 25. (*Pangonia*) M. P. Only a female remains in Paris and its labeling indicates it may not be the ♀ studied in 1845. The description was mainly based on the male, which seems to have been a different species, as noted by Schiner (1868) and Szilady (1926). Kröber (1930j) as *Scione*, but his description indicates a different species. Schiner (1868) as genotype of *Diclisia*. The specimen in Mus. Paris is very close to **Sc. minor* Macq. (q.v.), but with frons a little wider, palps, subcallus, and legs uniformly brown, no median black patches on abdomen. It would seem that the validity of the name must rest on the description of the ♂ rather than the specimen in Paris.

- **inconspicuus* Wlk. 1848, List, 1: 171. (*Tabanus*) B. M. = *Chlorotabanus inanis* Fab., Kröber (1930c).
- **indecisus* Big. 1892, 5: 666. (*Atylotus*) B. M.(H) = *Tabanus* = **Atylotus simplex* Big. 1892, p. 667. Not **Tabanus simplex* Wlk. 1850. Kröber (1934) as *Tabanus*. (N.S.)
- **infuscatipennis* Macq. MS., Surc. 1919, Mes. Arc Mérid. Équat. Amér. du Sud, 10(2): 230. (*Tabanus*) M. P. 1 ♀ specimen under this name does not agree with description of *T. ruber* Macq., for which it is supposed to be a substitute name, or with specimens det. as *infuscatipennis* by Bequaert. The specimen in Paris has no labels on it, but stands under a box label reading "T. infuscatipennis Cat. Mus." with "Colombie" added in pencil. Contrary to Bequaert and Renjifo (1946) no description appears to have been based on this specimen. The specimens upon which Surcouf based his description of *T. ruber* Macq. were not found. Kröber (1934) does not list.
- **inornatus* Wlk. 1848, List, 1: 199. (*Chrysops*) B. M.(H) = *Diachlorus bivittatus* (Wied.) 1828, Ricardo (1901). Kröber (1934).
- **innoscens* Wlk. 1854, List, 5, Suppl. : 327. (*Tabanus*) B. M.(H) = *Cryptotylus pallidipalpis* Stone (1944) = *Tabanus aurora*, Bequaert (1926) and Kröber (1929c). Not **T. aurora* Macq. (N.S.)
- **intereus* Wlk. 1856, Dipt. Saund., 1, pt. 5: 450. (*Tabanus*) B. M.(H) = **Catachlorops fuscinevis* (Macq.) 1839. Kröber (1934). Barretto (1946). (N.S.)
- **interruptus* Macq. 1838, Dipt. Exot., 1: 156. (*Diabasis*) M. P. = *Diachlorus immaculatus* (Wied.) 1828, Lutz (1913). Kröber (1928b).
- **jamaicensis* Newst. 1909, Ann. Trop. Med. Parasit., 3: 465. (*Atylotus*) B. M.(H) = *Stenotabanus (Aegialomyia)*, Fairchild (1951a). Bequaert (1940) as (*Stenotabanus*).
- **latipalpis* Macq. 1850, Dipt. Exot., Suppl. 4: 25. (*Pangonia*) M. P.(H) = (*Pseudoscione*). Ricardo (1900) as *Diatomineura*. Enderlein (1922, 1925, 1929) as *Listrappa* genotype. Kröber (1930f) as *Parosca*; (1934) as *Listrappa*.
- **lativentris* Macq. 1838, Dipt. Exot., 1(1): 153. (*Tabanus*) M. P.(H) = *Rhabdotylus planiventris* (Wied.) 1828. Blanchard, in Gay (1852) records from Chile, probably in error. Kröber (1934) species incert. sedis. (N.S.)
- **lativitta* Wlk. 1848, List, 1: 184. (*Tabanus*) B. M. = *Tabanus obsoletus* Wied. 1828, Lutz (1907); Kröber (1934). Type headless.
- **leucothorax* Ric. 1900, Ann. Mag. Nat. Hist., ser. 7, 5: 179. (*Diatomineura*) B. M.(H) = (*Pseudoscione*). Kröber (1930f) as *Parosca*; (1934) as *Listrappa*.
- **limbatus* Big. 1892, 5: 642. (*Theriopectes*) B. M.(H) = **Dichelacera unifasciata* Macq. 1838, Brethes (1910); Kröber (1934); Barretto (1949b).
- **limbithorax* Macq. 1855, Dipt. Exot., Suppl. 5: 22. (*Pangonia*) B. M. = *Scaptia*. Kröber (1930f) as *Parosca*; (1934) as *Listrappa*. Ferguson (1924) concluded on the basis of comparison by Austen with type of *limbithorax* that *niveovittata* Ferg. and Henry was a synonym and hence the species Australian. Although Kröber (1930f, 1934) treated the species as Neotropical, he saw no material other than the type. It should be excluded from the Neotropical fauna.
- **limonus* Towns. 1897, Ann. Mag. Nat. Hist., ser. 6, 20: 21. (*Tabanus mexicanus* var.) B. M.(H) = **Cryptotylus longiappendiculatus* Macq. 1855.

- Knab (1916) as syn. of *luteoflavus* Bell. Not *Cryptotylus limonus* Fairchild (1940a). (N.S.)
- **litigiosus* Wlk. 1853, Dipt. Saund., 1:37. (*Tabanus*) B. M.(H) = *Phaeotabanus* Lutz and Neiva (1914); Bequaert (1924) genotype of *Phaeotabanus*. The ♀ in B. M. is now headless but agrees with current interpretations of the species and with Kröber's (1930b) description and figs. It should be taken as lectotype. The ♂ is a different species, unknown to me.
- **lividus* Wlk. 1848, List, 1:162. (*Tabanus*) B. M.(H) = *Tabanus importunus* Wied. 1828. Kröber (1934) as syn. of *T. viduus* Wlk. (N.S.)
- **longiappendiculatus* Macq. 1855, Dipt. Exot., Suppl. 5:32. (*Tabanus*) B. M.(H) = *Cryptotylus*. = *Tabanus luteoflavus* Bell. 1859. = **T. purus* Wlk. 1860. = **T. mexicanus* var. *limonus* Towns. 1897. = *T. pallidus* Kröb. 1930. = *T. pallidulus* Kröb. 1934. Kröber (1934) as (*Macrocormus*). (N.S.)
- **longipalpis* Macq. 1848, Dipt. Exot., Suppl. 3:9. (*Pangonia*) B. M. = *Histriosilvius* Kröber 1930d genotype; redescribes and figures type. Lutz (1909) as *Esenbeckia*; Ricardo (1900a) as *Diatomineura*; Enderlein (1925) as *Protosilvius*.
- **longipennis* Ric. 1902, Ann. Mag. Nat. Hist., ser. 7, 11:433. (*Diatomineura*) B. M. = (*Pseudoscione*) Lutz et al., 1918; Fairchild (1951a) genotype of *Pseudoscione*; Enderlein (1922); Kröber (1930k) as *Listrioscia*.
- **longirostris* Macq. 1847, Dipt. Exot., Suppl. 2:12. (*Pangonia*) B. M.(H) = *Fidena nigripes* (V. Roder) 1892, nom. nov. Not *Pangonia longirostris* Hardwicke 1825. Kröber (1933b) as *longirostris*. = ? *Erephopsis brevistria* Lutz 1909. The type also agrees with specimens in B. M. det. *aurifasciata* End. by Kröber.
- **loricornis* Kröb. 1931, Zool. Anz., 95(1-2):32. (*Fidena*) B. M.(H) = **Pangonia basalis* var. Wlk. 1854, List, 5, Suppl. 1:322, not **basalis* Wlk. 1848. Ricardo (1900a) says Walker's second *basalis* 1854 not same as his first. Kröber's type of *loricornis* is the second specimen discussed by Ricardo, not the type of Walker's 1854 description, though I believe the two are conspecific.
- **lucidulus* Wlk. 1848, List, 1:188. (*Tabanus*) B. M. = **Tabanus obliquus* Wlk. 1850. Not *T. lucidulus*, Fchld. (1951a) and not *T. lucidulus* Austen in litt., Bequaert (1940), the latter = *T. obumbratus* Beq. 1940. The synonymy of the three Jamaican species of this group appears to stand as follows: (1) **T. lucidulus* Wlk. 1848 = **T. obliquus* Wlk. 1850. = *T. lucidulus* Kröb. 1930. (2) *T. townsendi* Johns. = **T. angustifrons* Towns. not Macq. = **T. lucidulus* Bequaert in part 1940. = **T. lucidulus* Fchld. 1951. (3) *T. obumbratus* Beq. 1940 = **T. lucidulus* Austen in litt. The true *lucidulus* does not appear to have been seen by Bequaert. It has a narrower frons, small oval callus less than half width of frons and unconnected with the median ridge, as figured by Kröber. Wings quite heavily fumose.
- **luctuosus* Macq. 1838, Dipt. Exot., 1(1):319. (*Tabanus*) B. M. = *Catachlorops*, Kröber (1934). Barretto (1946) with *nigripennis* Kröb. 1931 as synonym. The type from Brazil has wings wholly black, with all cells fenestrated; the specimen from Surinam is different, with apex of wing hyaline. Kröber (1939) seems to have used a form similar to the Surinam species in his redescription of *luctuosa*. His *nigripennis*, from description and figures, is composite, the description agreeing fairly well with *luctuosa*, the figures not.

- **Iugubris* Macq. 1838, Dipt. Exot., 1(1):108. (*Pangonia*) M. P. = *Esenbeckia*, Lutz (1909). Kröber (1934).
- **Iutzi* Surc. 1921, Gen. Insect., Taban. p. 54; 1923, Ann. Ent. Soc. France, 91(3):242. (*Stigmatophthalmus*) M. P. = *Dasychela*. Close to **D. riveti* Surc. Kröber (1940) as *Di cladocera* (*Stigmatophthalmus*). *St. altivagus* Lutz, the genotype, is quite different. Not listed by Kröber (1934).
- **macroceratus* Big. 1892, 5:687. (*Tabanus*) B. M.(H) = **Pseudacanthocera sylveirii* (Macq.) 1838. Kröber (1934).
- **macrodonta* Macq. 1839, Dipt. Exot., 1(2):183. (*Tabanus*) M. P.(H) = *Psalidia furcata* (Wied.) 1828, Lutz (1907).
- **macula* Macq. 1845, Dipt. Exot., Suppl. 1:43. (*Tabanus*) B. M.(H) = **Dasychela auribarbis* Macq. 1847. Kröber (1940) as *Di cladocera*, with *auribarbis*, *argyrophorus* Schin. 1868 and *scutellatus* Macq. 1839 as synonyms. Bequaert and Renjifo (1946) as *Dasychela* with *auribarbis* Macq., *argyrophorus* Schin. and *submacula* Wlk. 1850. The type of *scutellatus* Macq. could not be found, but I doubt its identity with *macula*. The type of **submacula* Wlk. is somewhat different though closely related.
- **maculifrons* Kröb. 1931, Stett. Ent. Zeitg., 92:277. (*Agclanius* (*Archiplatius*)) B. M.(H) = **Dasybasis maculiceps* (Kröb.) 1934, nom. nov. Not *Tabanus maculifrons* Hine 1907.
- **maculinevis* Macq. 1855, Dipt. Exot., Suppl. 5:31. (*Tabanus*) B. M. Kröber (1930a, 1934) as *Stypommisa*. Near **fulviventris* Macq. (q.v.).
- **maculipennis* Kröb. 1929, Zool. Anz., 83(1-4):52. (*Stypommia*); op. cit., (5-8):117. (*Stypommisa*) B. M.(H) = **Stenotabanus venosus* Big. 1892. Not *Tabanus maculipennis* Wied. 1828, Brullé 1832, Macquart 1834, or Macquart 1846.
- **maculiventris* Macq. 1850, Dipt. Exot., Suppl. 4:33. (*Tabanus*) M. P.(H) = *Dasybasis*. Kröber (1934) as *Tabanus*, with *rubromaculatus* Blanch. 1852 as synonym. The type is labeled "*rubromarginatus* Gay Chili," probably a lapsus for *rubromaculatus*, as well as with its published name, so that all three names refer to same specimens.
- **maletectus* Big. 1892, 5:664. (*Atylatus*) B. M. Kröber (1934) as *Tabanus*. The subepaulets are bare, labella fleshy, eyes bare, antennae missing. Frons broad with large black callus filling lower third of frons. Perhaps best in *Dasybasis*, but I do not recognize the species.
- **mallophoroides* Wlk. 1857, Trans. Ent. Soc. London, IV, 5:123. (*Tabanus*) B. M. = **Stibasoma dyridophorum* Knab 1913, Bequaert (1944). Lutz (1915) as *Stibasoma*. Kröber (1934) as *Stibasoma*. *Dyridophorum* has less yellow on dorsum of abdomen but otherwise same. It is possible that *festivum* Wied. and *panamense* Curr. are but races or color forms of the same species.
- **manifestus* Wlk. 1850, Dipt. Saund., 1:41. (*Tabanus*) B. M. = *Tabanus quinquevittatus* Wied. 1821, fide Philip in litt.
- **marginata* Macq. 1847, Dipt. Exot., Suppl. 2:14. (*Dichelacera*) B. M.(H) = **Dichelacera hinnulus* Wlk. 1850, Ricardo (1904). Lutz (1915).
- **marginatus* Macq. 1848, Dipt. Exot., Suppl. 3:172. (*Tabanus*) B. M. = *Tabanus*. Not *Tabanus marginatus* Wlk. 1848 (November) Australia. Ricardo's (1901) transference of Walker's species to *Silvius* makes it also a homonym of *marginatus* Macq. 1838. Kröber (1934) confused with *Silvius marginatus* Macq. 1838. The type is fragmentary and probably unidentifiable with certainty.

- **marginatus* Macq. 1838, Dipt. Exot., 1(1), pl. 19, fig. 1. (*Silvius*) M. P. = **Pseudacanthocera sylveirii* (Macq.) 1838, 1, c.p. 155. Not *Silvius marginatus* (Wlk.) Ricardo 1901. Both Macquart names almost surely were based on the same specimens; the types show only "*marginatus*," the name appearing on the figure, so it seems probable that the name was changed to honor the collector Sylveira shortly before publication but after the plates were made. Lutz (1907) as syn. of *Acanthocera coarctata* Wied.
- **marmorata* Big. 1892, 5:634. (*Dichelacera*) B. M.(H) = *Catachlorops potator* Wied. 1828; Kröber (1934).
- **minor* Macq. 1847, Dipt. Exot., Suppl. 2:29. (*Pangonia*) B. M.(H) = Scione. Kröber (1930j) with *aurea* Szil. and *incompleta* Macq. as synonyms, but description drawn from other material than the type. His treatment confusing, and I surmise he intended to synonymize *incompleta* Schiner, not *incompleta* Macq. with *minor* Macq.
- **minor* Macq. 1850, Dipt. Exot., Suppl. 4:33. (*Tabanus*) M. P. = *Dasybasis*. Kröber (1930i, 1934) as (*Agelanius*).
- **misera* O. S. 1886, Biol. Centr.-Amer., Dipt., 1:47. (*Diclisia*) B. M.(H) = Scione *aurulans* (Wied.) 1828, Hine (1925). Fairchild (1942d).
- **missionum* Macq. 1839, Dipt. Exot., 1(2):186. (*Tabanus*) M. P. = *Dasybasis*. Lutz et al. (1918) as *Neotabanus*.
- **modestus* Kröb. 1931, Stett. Ent. Zeitg., 92(1-2):293. (*Tabanus* (*Agelanius*)) B. M. = *Dasybasis modestinus* Kröb. 1934, nom. nov. Not *T. modestus* Wied. 1828.
- **montium* Surc. 1919, Mes. Arc Mérid. Équat. Amér. du Sud, 10:229. (*Tabanus*) M. P. = *Dasybasis*. Bequaert and Renjifo (1946) as *Agelanius*. Near *osornoi* Beq. and *excelsus* Surc.
- **multifascia* Wlk. 1850, Dipt. Saund., 1:68. (*Dichelacera*) B. M.(H) = *Dichelacera cervicornis* (Fab.) 1805; Ricardo (1904).
- **nana* Wlk. 1850, Dipt. Saund., 1:11. (*Pangonia*) B. M. = *Pseudelaphella*. Genotype, Kröber (1930e).
- **neglectus* Will. 1901, Biol. Centr.-Amer., Dipt., 1, Suppl. :256. (*Chrysops*) B. M.(H) = *Chrysops latifasciata* Bell., Hine (1925). Kröber (1934) as synonym of *C. incisa* Macq.
- neo-submacula* Kröb. 1931, Rev. Ent., 1(4):4-9. (*Dasyrhamphis*) B. M. Specimens so det. by Kröber in B. M., not types, which are in Berlin, agree with a specimen labeled "*Tabanus macula* var. n. sp." by Macquart in B. M. This specimen, though labeled as a type, appears not to have formed the basis of any published description. **Submacula* Wlk. and **macula* Macq. are conspecific and distinct from *neo-submacula* det. Kröber.
- **nigra* Kröb. 1931, Rev. Ent., 1(3):290. (*Rhamphidommia*) B. M. = *Amphichlorops Barretto* (1948).
- **nigrifascies* Big. 1892, 5:607. (*Mycteromyia*) B. M. = ? *Fidena*. The type is in execrable condition, but is not *Mycteromyia* and is probably not from India as described.
- **nigripennis* Guérin Meneville 1835, Icon. Regne Animal, Insectes, pl. XCVII, fig. 2; 1838, Voy. Coquille, Zool., II:288. (*Pangonia*) M. P. The specimen is labeled "*Pangonia nigripennis* nob. nov. sp." in Macquart's hand and bears a Guérin-Meneville label, so may be the type. It is congeneric and possibly conspecific with *Fidena aureosericea* Kröb., but is not the same as *piceohirta* Wlk. *Nigripennis* and *piceohirta* are placed as synonyms of *Sackenimyia*

- venosa* (Wied.) 1821 by Kröber (1930g, 1934). The palpi are very small and deeply grooved. = **Fidena**.
- **nigrithorax* Kröb. 1930, Zool. Anz., 90(3-4): 75. (*Diachlorus*) B. M. A ♀ in B. M. from Br. Guiana is close but lacks median black on third tergite. It stands over the box label *podagricus* Fab.
- **nigriventris* Kröb. 1931, Zool. Anz., 94(9-10): 254. (*Esenbeckia*) B. M.(H).
- **nigrivittata* Macq. 1850, Dipt. Exot., Suppl. 4: 23. (*Pangonia*) M. P. = **Fidena marginalis** (Wied.) 1830, Lutz (1907, 1909); Kröber (1933b, 1934). The synonymy is probable but not certain as there are several similar species here.
- **nigrohirta* Wlk. 1848, List, 1: 132. (*Pangonia*) B. M. = **Fidena venosa** (Wied.). Kröber (1930g).
- **nitens* Big. 1892, 5: 609. (*Mycteromyia*) B. M.(H) = **Fidena**. Kröber (1933b) redescribes, but his description and figures inconsistent and probably composite. Fairchild (1951a) genotype of *Bombylopsis* Lutz and *Ionopsis* Lutz.
- **nivalis* Wlk. 1850, Dipt. Saund., 1: 71. (*Scepsis*) B. M.(H) genotype. Surcouf (1921); Kröber (1928a).
- **notabilis* Wlk. 1850, Dipt. Saund., 1: 18. (*Pangonia*) B. M. = **Esenbeckia**, Kröber (1932a) with *inframaculata* Lutz as synonym. If *notabilis* and *inframaculata* are really synonymous, the species will go in *Proboscoides* Philip, but since the type of *notabilis* lacks the proboscis, this is uncertain. See Fairchild (1951a, p. 445).
- **nuntius* Wlk. 1854, List, 5, Suppl. 1: 207. (*Tabanus*) B. M.(H) = ***Tabanus desertus** Wlk. 1850. (N.S.) Kröber (1934) says type lost. Philip (1952) as synonym of *obsoletus* Wied., fide Hine MS.
- **obesus* Big. 1892, 5: 660. (*Atylotus*) B. M. The type is headless. The bare subepaulets, large size, 14 mm., and general fascies suggest *Dasybasis*, but I know of nothing resembling it from Mexico or Central America.
- **obliquus* Wlk. 1850, Dipt. Saund., 1: 28. (*Tabanus*) B. M. = ***Tabanus lucidulus** Wlk. 1848.
- **obscurhirta* Kröb. 1930, Zool. Anz., 86 (11-12): 284. (*Tabanus* (*Phacotabanus*) *aphanoptera* var.) B. M. Kröber (1934) as var. *obscuripilis*, nom. nov. Not *T. obscurhirta* Ric. 1908. = **Phaeotabanus obscuripilis** Kröb.
- **obscuriventris* Kröb. 1930, Zool. Anz., 87(1-2): 6. (*Tabanus* (*Macrocermus*)) B. M. = ***Tabanus** (*Lophotabanus*) *albocirculus* Hine 1907. Kröber (1934) as *obscurigaster*, nom. nov. Not *T. obscuriventris* Kröber 1929. (N.S.)
- **ocellus* Wlk. 1848, List, 1: 143. (*Pangonia*) B. M. = **Dasychela**. Ricardo (1900a) noted it was a tabanine. Kröber (1930h) as *Tabanus*. Says an artifact. The species is close to *Triceratomyia* Bequaert, to *Dasychela limbataivena* End., and *Di cladocera badia* Kröb., and the detached head now with the specimen clearly belongs to it. The antennae are now lost.
- **ochraceus* Macq. 1850, Dipt. Exot., Suppl. 4: 36. (*Diabasis*) M. P.(H) = **Diachlorus bimaculatus** Wied. (N.S.) Not *D. ochraceus* Kröber 1928 which = ? *D. angustifrons* Kröb.
- **ochraceus* Macq. 1838, Dipt. Exot., 1(1): 149; 1846, op. cit., Suppl. 1: 42. (*Tabanus*) M. P. 2 ♀ types. One = **Cryptotylus unicolor** Wied., the other = **Amphichlorops flavus** Wied. (N.S.)
- **oculatus* Big. 1892, 5: 606. (*Chrysops*) B. M. = **Chrysops molesta** Wied. 1828, Ricardo 1901; Kröber (1926, 1934).

- **oculus* Wlk. 1848, List, 1: 157. (*Tabanus*) B. M.(H) = *Tabanus* (*Lophotabanus*). Kröber (1934) as *Bellardia*. Fairchild (1942b, 1953). Only the Honduras specimen is now in B. M.
- **ornativentris* Kröb. 1929, Konowia, 8 (2): 182. (*Hybostraba*) B. M.(H) = *Tabanus nebulosus* subsp. Kröber (1929, l.c.) lists as synonym of *Lophotabanus druzvestejni* Szil., a synonym of *nebulosus* de Geer. Fairchild (1942f) as synonym of *ferifer* Wlk. The species is, in my opinion, a darker and smaller race of *nebulosus*.
- **pachycephalum* Big. 1892, 5: 636. (*Stibasoma*) B. M. = **Stibasoma chionostigma* O. S. 1886. Fairchild (1940b).
- **pachypalpus* Big. 1892, 5: 631. (*Dichelacera*) B. M.(H) = *Tabanus*. Near *bigoti* Bell. and *validus* Hine. Same as *rufipennis* Macq. 1846 (Dipt. Exot., Suppl. 1: 41), specimen in B. M., but different from **rufipennis* Macq. 1838, types in Paris.
- **pallidefemorata* Kröb. 1930, Zool. Anz., 90: 72. (*Chrysops auroguttata* var.) B. M. = *Chrysops pallidefemorata*, Bequaert (1944); Pechuman (1937).
- **pallidinctus* Kröb. 1930, Zool. Anz., 86(11-12): 297. (*Tabanus* (*Phaeotabanus*)) B. M.(H) = *Tabanus* (*Philipotabanus*) *caliginosus* Bell., Fairchild (1953).
- **parallelus* Wlk. 1848, List, 1: 187. (*Tabanus*) B. M. = *Stenotabanus*, Bequaert (1940) with **T. alene* Towns. as synonym.
- **patellicornis* Kröb. 1930, Zool. Anz., 88(11-12): 307. (*Pseudelaphella*) B. M.(H).
- **pavida* Will. 1901, Biol. Centr.-Amer., Dipt., 1, Suppl. :253. (*Pangonia*) B. M. = *Esenbeckia*. Enderlein (1925) and Kröber (1934) as *Ricardoa*. Palpi long, curved, and deeply grooved outwardly. Philip (1954a).
- **penicillata* Big. 1892, 5: 610. (*Mycteromyia*) B. M. = *Fidena*. Lutz (1909) as *Erephopsis*, but probably not same species. Kröber (1930k) as *Melpia*; (1934) as *Fidena*. The only black species with reddish legs I have seen.
- **perplexus* Wlk. 1850, Dipt. Saund., 1: 32. (*Tabanus*) B. M.(H). Kröber (1940) as *Diadocera*. The subepaulets are setose and the species belongs with *hirtitibia* Wlk. in the group treated as *Chelommia* by Barretto (1949a).
- **peruviana* Big. 1892, 5: 635. (*Dichelacera*) B. M.(H) = ? *Dasychela limbaticena* End. 1925. The subepaulets are bare and the specimen resembles *Dasychela badia* Kröber.
- **peruvianus* Macq. 1848, Dipt. Exot., Suppl. 3: 173. (*Tabanus*) B. M.(H). The specimen has the first posterior cell closed, a fact not mentioned in the original description, and may not be the true type. The subepaulets are setose. Kröber (1931c) as *Gymnochela*; (1934) as *Chelommia*. Barretto (1949a) as *Chelommia*. Bequaert and Renjifo (1946) as *Dichelacera* (*Psallidia*).
- **picco-hirta* Wlk. 1848, List, 1: 132. (*Pangonia*) B. M. = *Fidena venosa* Wied.
- **pictipennis* Macq. 1834, Hist. Nat., Dipt., 1: 199. (*Tabanus*). 2 ♀ ex coll. Bigot in B. M. under *Acanthocera longicornis* Fab. bearing labels "Brazil ex coll. Serville" which may be types of *pictipennis*. As noted by Fairchild (1939) the description agrees well with *longicornis*. (N.S.) Not listed by Kröber (1934).
- **pictipennis* Macq. 1850, Dipt. Exot., Suppl. 4: 32. (*Tabanus*) M. P. = ? *Catachlorops*. May be a teneral specimen of a well-known species. Kröber (1934) as synonym of *Tabanus uruguayensis* Lynch-Arrib. 1882. Not
- **Tabanus pictipennis* Macq. 1834. Not *Catachlorops pictipennis* Kröb. 1931.

- **pictus* Kröb. 1930, Zool. Anz., 86(11-12): 264. (*Eutabanus*) B. M. Subepaulets bare. Nearest *Stenotabanus* but distinct. Bequaert (1939).
- **plangens* Wlk. 1854, List, 5, Suppl. 1: 199. (*Tabanus*) B. M.(H) = *Tabanus lineola* var. Fairchild (1942c).
- **polytaenia* Big. 1892, 5: 667. (*Atylotus*) B. M.(H) = **Tabanus angustus* Macq. 1838, Kröber (1934).
- **praetereuns* Wlk. 1850, Dipt. Saund., 1: 69. (*Dichelacera*) B. M. = *Catachlorops*. Closest to *halteratus* Kröb. and *d'almeidai* Pech. Lutz et al. (1918). Barretto (1946) in key only.
- **primitivus* Wlk. 1848, List, 1: 177. (*Tabanus*) B. M. Lutz (1907) = *trivittatus* Latr. Kröber (1930c) as *Macrocornus*, redescribes. Near *strigimaculus* Fchld. 1942.
- **pruinus* Kröb. 1931, Stett. Ent. Zeitg., 92(2): 276. (*Tabanus* (*Agelanius*)) B. M.(H) = *Dasybasis*. Kröber (1934) as *pruinivitta*, nom. nov. Not *T. pruinus* Big. 1892, or Hine 1900, or Surcouf 1906, or Kröber 1929.
- **pubescens* Macq. 1847, Dipt. Exot., Suppl. 2: 20. (*Tabanus*) B. M. The type is in very bad condition, probably composite and not certainly Neotropical. Not *T. pubescens* Ström 1768 or Walker 1854.
- **pulchra* Will. 1901, Biol. Centr.-Amer., Dipt., 1, Suppl. : 263. (*Dichelacera*) B. M.(H) = *Dichelacera salvadorensis* Lutz 1915. (N.S.)
- **pulverulentus* Big. 1892, 5: 665. (*Atylotus*) B. M.(H) = *Tabanus olivaceiventris* Macq. 1847. (N.S.) = **Tabanus imponens* Wlk., Kröber (1929a).
- **pumiloides* Will. 1901, Biol. Centr.-Amer., Dipt., 1, Suppl. : 260. (*Tabanus*) B. M. = *Stenotabanus*. Fairchild (1953).
- **punctipennis* Macq. 1838, Dipt. Exot., 1(2): 185. (*Tabanus*) M. P.(H) = *Tabanus* (*Hybomitra*) *quadripunctatus* Fab. Fairchild (1942f). Not *T. punctipennis* Macq. 1847 (Nearctic), or *Stypommisa punctipennis* End. 1925.
- **purus* Wlk. 1860, Trans. Ent. Soc. London, 5: 274. (*Tabanus*) B. M.(H) = **Cryptotylus longiappendiculatus* Macq. 1855. Hine (1925) as synonym of *luteoflavus* Bell. (N.S.)
- **pyrausta* O. S. 1886, Biol. Centr.-Amer., Dipt., 1: 43. (*Pangonia*) B. M.(H) = *Fidena rhinophora* Bell. 1859, Fairchild (1953).
- **quadrimaculatus* Macq. 1845, Dipt. Exot., Suppl. 1: 39. (*Tabanus*) B. M. = *Dichelacera*. Kröber (1932a) as *Gymnochela*; says *poeciloptera* Schiner same; (1934) as *Amphichlorops*. Close to **testacea* Macq., and **alcis* Will.
- **reinburgi* Surc. 1919, Mes. Arc Mérid. Équat. Amér. du Sud, 10: 233. (*Esenbeckia*) M. P.
- **repanda* Wlk. 1848, List, 1: 190. (*Dichelacera*) B. M.(H) = **Dichelacera testacea* Macq. 1846, Kröber (1934).
- **reticulatus* Kröb. 1930, Zool. Anz., 86(11-12): 298. (*Tabanus* (*Phacotabanus*)) B. M.(H) = (*Philipotabanus*), Fairchild (1942f).
- **riveti* Surc. 1919, Mes. Arc Mérid. Équat. Amér. du Sud, 10: 226. (*Tabanus*) M. P. = *Dasychela*. Kröber (1940) as *Di cladocera*.
- **rubescens* Macq. 1838, Dipt. Exot., 1(1): 143. (*Tabanus*) M. P. = *Dasybasis*. Type headless and denuded, but not same as specimens ex coll. Bigot in B. M. so labeled. Near **trigonophorus* Macq. but probably now indeterminable.
- **rubescens* Big. 1892, 5: 663. (*Atylotus*) B. M. = *Tabanus campestris* Brethes 1911, nom. nov. Kröber (1933a) redescribes. Subepaulets setose. Not *rubescens* Macq. 1838, Bellardi 1859.

- **rubidus* Macq. 1847, Dipt. Exot., Suppl. 2: 19. (*Tabanus*) B. M. Not *T. rubidus* Wied. 1821. Kröber (1934) as *T. rubricosa*, nom. nov. Not *T. rubricosa* Wulp. 1881. Type headless and excessively dirty, probably now indeterminate. Near **fallax* Macq. and *albibarbis* Wied.
- **rubiginipennis* Macq. 1845, Dipt. Exot., Suppl. 1: 39. (*Tabanus*) B. M.(H) = **Tabanus adustus* Wlk. 1850. Kröber (1940) as *Di cladocera*. Bequaert and Renjifo (1946) as *Hybomitra*. Eyes bare, subepaulet setose. Near *bigoti* Bell.
- **rubiginosa* Summers 1911, Ann. Mag. Nat. Hist., ser. 8, 7: 213. (*Dichelacera*) B. M. = (*Psalidia*). Kröber (1934) as *Dichelacera*. Close to *fulminca* Hine, but with bicolored fore tibiae and widely open cell R5.
- **rubribarbis* Big. 1892, 5: 630. (*Atylotus*) B. M.(H) = *Dichelacera* (*Psalidia*) *furcata* (Wied.) 1828, Kröber (1932b).
- **rubrinotatus* Big. 1892, 5: 676. (*Atylotus*) B. M.(H) = **Tabanus guyanensis* Macq. 1845. Kröber (1934) does not mention. (N.S.)
- **rubripes* Macq. 1838, Dipt. Exot., 1(1): 138. (*Tabanus*) M. P.(H). The type is labeled "Sylveira Bresil 1832" though the original description says "Cayenne, Sylveira." All other Sylveira material was from Brazil, so I believe Macquart erred here in transcribing the locality. Kröber (1930c, 1934) as (*Macrocornus*). The species is close to *sorbillans*, but distinct. Specimens in B. M. det. Bigot are *sorbillans* Wied.
- **rubrithorax* Macq. 1838, Dipt. Exot., 1(1): 143. (*Tabanus*) M. P.(H) = *Stenotabanus*. Type headless, but appears to belong in group of *pequeniensis* Fchld. with a few setae on subepaulet.
- **rubriventris* Kröb. 1930, Mitt. Mus. Hamburg, 44: 165. (*Oscia*) B. M. = *Scaptia*.
- **rufa* Macq. 1847, Dipt. Exot., Suppl. 2: 13. (*Dichelacera*) B. M. = ? *Dichelacera submarginata* Lutz 1915. Rondani (1850) transfers to *Tabanus* and changes name to *brasiliensis*, nom. nov. Lutz (1907) = ? *D. januarii* var. Kröber (1934) = *januarii* Wied. A pale form with reduced wing markings and broad frons.
- **rufescens* Ric. 1900, Ann. Mag. Nat. Hist., ser. 7, 6: 294. (*Erephrosis*) B. M.(H). The holotype is in Budapest; this is a paratype. = **Scione aureopygia* Fchld. 1942. = **Fidena fulvosericea* Kröb.
- **ruficornis* Kröb. 1931, Stett. Ent. Zeitg., 92: 287. (*Tabanus* (*Agelanius*)) B. M. = *Tabanus erythrocerus* Kröb. 1934, nom. nov. Not *T. ruficornis* Fab. Subepaulet setose. Close to **desertus* Wlk. and **johannesi* Fchld.
- **rufipennis* Macq. 1838, Dipt. Exot., 1(1): 138. (*Tabanus*) M. P. = *Di cladocera*. Subepaulet bare, labella with sclerotized plate. Very close to **castanea* Big. and *unicolor* Lutz, and all may be variants of same species. **Satanica* Big. also close, but distinct.
- **rufipes* Macq. 1850, Dipt. Exot., Suppl. 4: 37. (*Silvius*) M. P. = ? *Veprius*. Type very dirty, 9-10 mm. Hind tibial spurs and ocelli present. Proboscis short and fleshy. Frons wider than high, divergent, callus transverse, barlike. Third antennal segment with a basal plate and probably four annuli.
- **rufithorax* Wlk. 1848, List, 1: 165. (*Tabanus*) B. M. = *Catachlorops*, Kröber (1934). Barretto (1946) in key only.
- **rufiventris* Macq. 1838, Dipt. Exot., 1(1): 145. (*Tabanus*) B. M. = **Tabanus bifloccus* Hine 1925. Not *T. rufiventris* Fab. 1805 or Macquart 1845. Kröber (1934) does not list. Bequaert (1940) = ? *T. hookeri* Knab.

- **rufiventris* Macq. 1845, Dipt. Exot., Suppl. 1: 38. (*Tabanus*) B. M. = **Tabanus simplex* Wlk. 1850. Not *T. rufiventris* Fab. 1805 or Macq. 1838. = *Tabanus (Hybomitra) indiorum* Beq. and Renjifo 1946, nom. nov. pro *rufiventris* Macq. 1845. (N.S.)
- **rufohirta* Wlk. 1848, List, 1: 131. (*Pangonia*) B. M.(H) = *Fidena venosa* (Wied.), Kröber (1930g, 1934).
- **rufopilosus* Big. 1892, 5: 620. (*Veprius*) B. M. Ricardo (1901) as *Silvius*. Kröber (1930d, 1934) lists under *Veprius* with a query. Hind tibial spurs, bare subepaulet and subcosta, fleshy labella, and pilose holoptic eyes.
- **rufus* Kröb. 1931, Stett. Ent. Zeitg., 92: 287. (*Archiplatus*) B. M.(H) = **Tabanus desertus* Wlk. Not *T. rufus* Scop. 1763 or Palisot de Beauvois 1809. Kröber (1934) as *T. (Agclanius) ruficolor*, nom. nov. (N.S.)
- **satanica* Big. 1892, 5: 632. (*Dichelacera*) B. M. = *Di cladocera*. Kröber (1931c) as *Gymnochela* with *castanea* Big. as syn.; (1934) as *Chelommia*. The subepaulets are bare and the species congeneric with *unicolor* Lutz and **rufipennis* Macq. It also agrees well with the description of *T. scutellatus* Macq., but the type of the latter could not be found at B. M. or Paris. Barretto (1948) as *Amphichlorops* with *castanea* Big. as synonym.
- **scapularis* Macq. 1847, Dipt. Exot., Suppl. 2: 15. (*Dichelacera*) B. M.(H). Hine (1917). Kröber (1934). Nearest to **marginata* Macq.
- **scutellata* Macq. 1838, Dipt. Exot., 1(1): 155. (*Diabasis*) M. P.(H) = *Diachlorus*. Kröber's (1928b) redescription and figure not accurate. Frons parallel-sided, callus weakly trifold above.
- **scutellatus* Kröb. 1931, Ann. Mus. Hung., 27: 348. (*Cotachlorops*) B. M. Barretto (1946) keys out with *rufescens* Fab.
- **scutulatus* Kröb. 1930, Dipt. Pat. S. Chile, 5(2): 143. (*Theriopectes*) B. M.(H) = *Dasybasis*. = **Tabanus (Theriopectes) albovittatus* Kröb. 1930. (N.S.) Kröber (1934) as *Sziladymus*.
- **seminigra* Ric. 1902, Ann. Mag. Nat. Hist., ser. 7, 9: 432. (*Diatomineura*) B. M. = (*Pseudoscione*). Lutz (1907) and Kröber (1934) as synonym of *Listrapha tabanipennis* Macq. The type of **tabanipennis* in Paris is a *Fidena*. Specimens det. *tabanipennis* by Bigot in B. M. are *seminigra* Ric. Close to **fenestrata* Macq. and **longipennis* Ric.
- **semisordidus* Wlk. 1854, List, 5: 208. (*Tabanus*) B. M.(H) = *Tabanus importunus* Wied., Kröber (1929c, 1934).
- **semiviridis* Ric. 1900, Ann. Mag. Nat. Hist., ser. 7, 8: 181. (*Pangonia*) B. M.(H) = *Esenbeckia prasiniventris* Macq., Bequaert and Renjifo (1946). Kröber (1932a, 1934). Described as from Barengo, Old Castile, Spain, but the original label is indecipherable and might have been "Venezuela."
- **senior* Wlk. 1850, Dipt. Saund., 1: 67. (*Tabanus*) B. M.(H) = *Tabanus albarbis* Wied. 1824. (N.S.) Bodkin and Cleare (1916). Kröber (1934) not listed.
- **shannoni* Kröb. 1930, Dipt. Pat. S. Chile, 5(2): 144. (*Theriopectes*) B. M. = *Dasybasis*.
- **simplex* Wlk. 1850, Dipt. Saund., 1: 34. (*Tabanus*) B. M. = **Tabanus rufiventris* Macq. 1845. Not *T. rufiventris* Fab. 1805. = *Tabanus (Hybomitra) indiorum* Bequaert and Renjifo 1946. (N.S.) Kröber (1934) suggests = *biflocus* Hine, but confusion here with *rufiventris* Macq. 1838. Fairchild (1942a) under *umbraticolus*, which is entirely distinct.

- **simplex* Big. 1892, 5:667. (*Tabanus*) B. M.(H) = **Tabanus indecisis* (Big.) 1892. Not **T. simplex* Wlk. (N.S.) Kröber (1934) = ? *T. (Neotabanus) signativentris* Brethes. There are three cotypes, the lectotype being the one with the Bigot name label. The other two are different species.
- **sparsa* Wlk. 1850, Dipt. Saund., 1:71. (*Dichelacera*) B. M.(H) = *Dicladocera guttipennis* (Wied.) 1828, Lutz (1907). Eyes sparsely pilose.
- **stigmatalis* Kröb. 1931, Stett. Ent. Zeitg., 92:299. (*Tabanus*) B. M.(H) = **Tabanus (Philopotabanus) grassator* Fchld. 1953. Type headless. My specimen becomes allotype. (N.S.)
- **subfascipennis* Macq. 1855, Dipt. Exot., Suppl. 5:35. (*Chrysops*) B. M. = *Chrysops variegata* de Geer. Kröber (1934) as var. of *variegata*. A large dark form, wing apex unusually dark and outer border of crossband concave.
- **submacula* Wlk. 1850, Dipt. Saund., 1:30. (*Tabanus*) B. M.(H) = *Dasychela*, Bequaert and Renjifo (1946) who place as synonym of *macula* Macq. Kröber (1931b) as synonym of *neo-submacula* Kröb. 1931; (1934) places in synonymy of both *macula* Macq. and *neo-submacula* Kröb. Both the latter are distinct species, in my opinion.
- **subvaria* Wlk. 1848, List, 1:150. (*Tabanus*) B. M. = *Esenbeckia*, Kröber (1932a, 1934). Walker (1849) = *Pangonia fuscipennis* Wied. var. Ricardo (1900) = *Pangonia*, a distinct species. Close to **Esenbeckia notabilis* Wlk., the proboscis rather heavy, incompletely sclerotized.
- **sulphureus* Macq. 1847, Dipt. Exot., Suppl. 2:19. (*Tabanus*) B. M.(H) = *Chlorotabanus inanis* (Fab.), Kröber (1934). Lutz (1907) as a pale form of *mexicanus* L.
- **tabanipennis* Macq. 1848, Dipt. Exot., 1(1):108. (*Pangonia*) M. P. The lectotype = *Fidena castanea* Perty 1833 of Kröber (1930k). The specimen from de la Mana Leschen, a paratype, = ? **Pseudoscione seminigra* Ric. Specimens in B. M. det. *tabanipennis* by Bigot = *seminigra* Ric. The lectotype of *tabanipennis* also = **Fidena unicolor* Macq. 1845. (N.S.)
- **tanycerus* O. S. 1886, Biol. Centr.-Amer., Dipt., 1:46. (*Chrysops*) B. M.(H) = *Assipala* Philip 1941 genotype.
- **tenens* Wlk. 1850, Newman's Zoologist, 8, App., p. lxxv. (*Tabanus*) B. M.(H) = *Tabanus cinerarius* Wied. 1828. Not *T. tenens* Wlk. 1850, Dipt. Saund., 1:49. Walker (1854) changes name to *confligens*. Kröber (1934) as *Chelommia*. *T. cinerarius* was proposed as a new name for *T. glaucus* Wied. 1819 (Zool. Mag., 1(3):42) thought to be preoccupied by *T. glaucus* Meig. 1820 (Syst. Beschreib. Europ. Zweifl. Ins., 2:51) but this appears to be an error, and the species should be known as *Tabanus glaucus* Wied. 1819.
- **tenuirostris* Wlk. 1860, Trans. Ent. Soc. London, 5:272. (*Pangonia*) B. M. = *Esenbeckia flavohirta* Bell. 1859. Kröber (1934) as *Ricardoa flavohirta*.
- **tenuistria* Wlk. 1848, List, 1:143. (*Pangonia*) B. M. = *Fidena*. Kröber (1930g) as *Sacknomyia* redescibes type; (1934) as *Melpia*.
- **tepicana* Towns. 1912, Can. Ent., 44(1):287. (*Pangonia*) B. M. = *Esenbeckia*. Philip (1954a).
- **terminalis* Macq. 1855, Dipt. Exot., Suppl. 5:36. (*Chrysops*) B. M.(H) = *Diachlorus curvipes* Fab. 1805. (N.S.)
- **terminus* Wlk. 1848, List, 1:160. (*Tabanus*) B. M. = ? *Tabanus sorbillans* Wied. Type is a ♂ and seems to match *sorbillans* fairly well. Kröber (1933a) as a valid species of (*Neotabanus*). (N.S.)

- **testacea* Macq. 1846, Dipt. Exot., Suppl. 1: 29. (*Dichelacera*) B. M.(H). Kröber (1934) with *repanda* as queried synonym = **Dichelacera repanda* Wlk. 1848. Bequaert and Renjifo (1946) as (*Catachlorops*). Close to **quadrimaculatus* Macq. and **alcis* Will.
- **testaceiventris* Macq. 1848, Dipt. Exot., Suppl. 3: 9. (*Pangonia*) B. M.(H) = *Esenbeckia*, Kröber (1932a) with *umbra* Wlk. 1850 as synonym = **E. umbra* Wlk.
- **testaceomaculatus* Macq. 1838, Dipt. Exot., 1(1): 144. (*Tabanus*) M. P.(H) = *Dasybasis*, Kröber (1930i) as (*Agelanius*). = ? **D. trigonophorus* Macq. 1838, p. 185.
- **testaceus* Macq. 1838, Dipt. Exot., 1(1): 137. (*Tabanus*) M. P. Closest to **T. indecisis* Big. but differs. Kröber (1930c) claims he saw type in London. Not *T. testaceus* Forskal 1775.
- **tinctipennis* Kröb. 1931, Zool. Anz., 94(9-10): 256. (*Esenbeckia*) B. M.
- **tinctus* Wlk. 1850, Dipt. Saund., 1: 29. (*Tabanus*) B. M. = *Tabanus eggeri* Schin. 1868 (Palearctic), nom. nov. pro *T. intermedius* Egger 1859, not Walker 1848. Walker's name appears to be the oldest for this European species. Bequaert (1940) suggests may not be Neotropical. (N.S.)
- **transposita* Wlk. 1854, List, 5: 151. (*Dichelacera*) B. M.(H) = *Catachlorops*, Kröber (1931i, 1934). Fairchild (1940b).
- **trifaria* Macq. 1838, Dipt. Exot., 1(1): 163. (*Chrysops*) M. P.(H). Kröber (1926, 1934).
- **trifascia* Wlk. 1850, Dipt. Saund., 1: 37. (*Tabanus*) B. M. Type in very poor condition, a ♂ *Stenotabanus*, but not further identifiable in present state of knowledge of this group. It is not the ♂ of **callosus* Macq. as suggested by Kröber (1934).
- **trigonophorus* Macq. 1838, Dipt. Exot., 1(2): 185. (*Tabanus*) M. P. = *Dasybasis*. Very close to **testaceomaculatus* Macq. 1838, p. 144, structurally, but both types very denuded and certainty impossible.
- **tristis* Big. 1892, 5: 621. (*Dasybasis*) B. M. = ? *Protodasyapha*, Kröber (1930k). A ♂. Eyes densely pubescent, holoptic, facets demarcated. Ocelli present. Subepaulet bare, hind tibiae spurred, labella fleshy, antennae subulate, *Pangonia*-like.
- **tritus* Wlk. 1857, Trans. Linn. Soc. London, 17(3): 338. (*Tabanus*) B. M. = *Dasybasis*. Kröber (1930i, 1934) as *Stypommia*, the genotype of which *St. patagonica* End., he considers a synonym of *tritus* Wlk., but his figures and descriptions of *patagonica* and *tritus* do not agree with each other or with Walker's type.
- **umbra* Wlk. 1850, Dipt. Saund., 1: 19. (*Pangonia*) B. M.(H) = **Esenbeckia testaceiventris* Macq. 1848, Kröber (1934).
- **unicinctus* Wlk. 1857, Trans. Ent. Soc. London, 4: 122. (*Tabanus*) B. M. = **Leucotabanus albovarius* (Wlk.) 1854. (N.S.) = **Leucotabanus leuconotum* Fchld. 1941. Not *T. unicinctus* Loew 1856. The type lacks antennae and is poorly preserved. It is either *albovarius* Wlk. or *canithorax* Fchld. with the former more likely. **Leuconotum* Fchld. is the same as **albovarius* Wlk.
- **unicolor* Macq. 1845, Dipt. Exot., Suppl. 1: 27. (*Pangonia*) B. M.(H) = *Fidena castanea* Perty 1830, Kröber (1930k, 1934). = **Pangonia tabanipennis* Macq. 1848. Lutz (1909) makes *xanthopogon* Macq. 1838 also a synonym of *castanea* Perty. Lutz (1907) says *unicolor* Will. 1895 is different.

- **unifasciata* Macq. 1838, Dipt. Exot., 1(1):119. (*Dichelacera*) M. P.(H). Barretto (1949b) with **limbata* Big., *trigonotacnia* Lutz and *soror* Kröb. as syns.
- **unipunctatus* Big. 1892, 5:663. (*Atylotus*) B. M.(H) = **Tabanus* (*Lophotabanus*) *piraticus* Fchld. 1942. (N.S.) Philip (1952) = *T. jilamensis* Hine. Not *T. (L.) unipunctatus*, Kröb. 1929. *Jilamensis* Hine appears to be distinct. See Fairchild 1942a.
- **univittatus* Macq. 1855, Dipt. Exot., Suppl. 5:30. (*Tabanus*) B. M.(H) = **Tabanus desertus* Wlk. 1850. (N.S.)
- **vacillans* Wlk. 1850, Dipt. Saund., 1:70. (*Dichelacera*) B. M.(H) = ? *Catachlorops capreolus* Wied. 1828. (N.S.) Kröber (1934) as synonym of *potator* Wied. 1828. Not *vacillans*, Barr. 1946. The type keys out to *capreolus* in Barretto's key (1946). Lutz (1907) = *potator* Wied.
- **valterii* Macq. 1838, Dipt. Exot., 1(2):184. (*Tabanus*) M. P. Related to *cinerarius* Wied. and *importunus* Wied. but apparently distinct.
- **varius* Wlk. 1848, List, 1:209. (*Diabasis*) B. M.(H) = *Scaptia*. Ricardo (1904) as ? *Diatomincura*. Kröber (1930k) = *Calliosca schoenemanii* End. genotype.
- **varipes* Wlk. 1854, List, 5, Suppl. 1:298. (*Chrysops*) B. M.(H) = *Dia-chlorus curvipes* Fab. 1805, Ricardo (1901).
- **varipes* Wlk. 1857, Trans. Linn. Soc. London, 17(3):337. (*Tabanus*) B. M. Kröber (1934) = ? ? *Tabanus*. Subepaulet setose, a small vertical tubercle, eyes sparsely short pilose under high magnification. Looks Nearctic or Palearctic to me.
- **venenatus* O. S. 1886, Biol. Centr.-Amer., Dipt., 1:53. (*Tabanus*) B. M.(H) = *Rhabd tylus*. Kröber (1934) = *Amphiclorops*. Fairchild (1942b) = *Stibasoma*. Very close to **Rhab. viridiventris* Macq.
- **venosus* Big. 1892, 5:685. (*Tabanus*) B. M.(H) = **Stenotabanus maculipennis* (Kröb.) 1929. (N.S.) Kröber (1930a) as *Stypommia*, but his *venosus* not same species as the type. *St. pequenicensis* Fchld. 1942 also close.
- **viduus* Wlk. 1850, Newman's Zoologist, 8, App., p. lxviii. (*Tabanus*) B. M.(H) = **Tabanus basivitta* Wlk. 1850. (N.S.) Kröber (1930h) = *T. (Lophotabanus) lividus* Wlk. 1848, but this latter = *importunus* Wied., in my opinion.
- **viridiventris* Macq. 1838, Dipt. Exot., 1(1):112. (*Pangonia*) M. P.(H) = (*Pseudoscione*). Enderlein (1922, 1925) as *Parosca* genotype. Kröber (1930k) as *Parosca*; (1934) as *Listrapha*.
- **viridiventris* Macq. 1838, Dipt. Exot., 1(1):141. (*Tabanus*) M. P.(H) = *Rhabd tylus*. Close to *venenatus* O. S. and *planiventris* Wied. Carrera and Lane (1945).

SUMMARY

A study of the type specimens of Neotropical Tabanidae preserved in the British Museum of Natural History in London and the Muséum d'Histoire Naturelle in Paris is reported. The types or type material of 335 species were seen and an attempt made to place them generically. New synonymy is proposed in about 70 cases and new generic or subgeneric placement in 76 cases. Three new names are proposed

for homonyms and four species previously considered Neotropical are shown to be probably or surely from other regions. Specimens compared and agreeing with the types of 181 names (homotypes) were brought back and will eventually be deposited in American museums. Of the names treated, 189 appear to be valid, pending complete information on the status of the earlier names of Wiedemann, Thunberg, and some other authors; 110 are synonyms, and 40 are homonyms—in a fair number of cases a name may be both. In a few cases it was impossible to fix the status of a name owing to the condition of the type or uncertainty as to the material's being a true type. For the sake of completeness a list is also given of the Walker and Macquart species and a few others whose types could not be found—64 in all. The Walker types are presumed lost, while some of the Macquart types not seen by me are in Paris and others may turn up elsewhere.

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SMITHSONIAN MISCELLANEOUS COLLECTIONS
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NEW CRETACEOUS BRACHIOPODA
FROM ARIZONA

(WITH 4 PLATES)

By
G. ARTHUR COOPER
United States National Museum
Smithsonian Institution



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(WITH FOUR PLATES)

Cretaceous brachiopods, except for the occurrences of *Kingena* in Texas, are a great rarity in the United States, and it is also unusual to find here more than one kind of brachiopod of that age in abundance. However, in 1947, Dr. J. B. Reeside, Jr., of the U. S. Geological Survey, called my attention to several species of brachiopods from the Cretaceous Mural limestone of Arizona. These were insufficient for study; therefore, in the summer of that year I went to the Bisbee area of Arizona with Dr. Ellis Yochelson, now of the U. S. Geological Survey, to obtain more material.

Occurrence of Cretaceous brachiopods in Arizona is mentioned by Ransome (1904, p. 6) in his description of the Bisbee Quadrangle. The single occurrence cited is said to be the only one on the quadrangle and is a small hill on the east side of the quadrangle opposite the mouth of Glance Canyon and about 3 miles east of Glance. This hill is in the NW $\frac{1}{4}$ SW $\frac{1}{4}$ NE $\frac{1}{4}$ sec. 36, T. 23 S., R. 25 E. and lies about 0.2 mile east of U. S. Highway 80 about 12.7 miles west-northwest of Douglas, Cochise County. The location is thus easily accessible because of its proximity to an excellent road, and it is from this locality that Dr. Yochelson and I collected the specimens described below.

The low hill from which the brachiopods were taken consists of massive limestone, through which the brachiopods are scattered. They are not concentrated in bands, although some pieces were found in which they were fairly common. A large part of the collection consisted of small lumps showing one or two specimens. Although some large pieces were taken, they were not rich and it was best, therefore, to collect individual specimens or small groups in small pieces. The limestone lumps taken produced few specimens aside from brachiopods. These included small oysters, small rudistids, and a few poorly

preserved small echinoids. The brachiopods are fairly well silicified. The silicification is not coarse or crude in the large specimens, but it is in some of the immature ones. In general the specimens are brittle and fragile and must be handled with great care.

These brachiopods occur in the Mural limestone but, because of the isolated character of the hill, the exact stratigraphic position of the specimens is uncertain. Ransome, who defined the Mural, states that "The little hills near the eastern edge of the quadrangle north of Hay Flat are composed mainly of the hard limestones of the upper member of the formation. Some of the beds here contain abundant corals (*Astrocenia* and another form not collected). *Caprina*, and a number of little brachiopods (*Rhynchonella*, *Terebratella* and *Terebratula*) not seen at any other locality in the quadrangle."

Stoyanow (1949, p. 20) divides the Mural limestone into three units: (a) Basal thinner-bedded limestone with *Orbitolina texana*; (b) massive "rudistid" limestone, and (c) thinner-bedded limestone with *Orbitolina texana*. He says: "In the basal beds of the Mural limestone, small brachiopods, corals, specimens of *Lima muralensis*, and large forms of *Lunatia*? sp. often occur. The massive limestone is usually replete with *Radiolites*? sp., whereas the specimens of *Caprina* sp. are comparatively rare and come from the thinner-bedded layers below the reef." These remarks suggest that Stoyanow identified the brachiopod beds as low in the Mural. Perhaps brachiopods occur in more than one level and were not seen by Ransome. At any rate the Mural limestone is now placed (Cobban and Reeside, 1952) at about the middle of the Albian stage in the Lower Cretaceous.

CRANISCUS HESPERIUS Cooper, new species

Plate 3A, figures 1-3

Pedicle valve unknown.

Brachial valve a low cone about medium size for the genus, sub-rectangular in outline; length about two-thirds the width; maximum width in anterior third; sides slightly oblique and gently rounded; anterior margin broadly rounded; anterolateral extremities narrowly rounded; posterior margin nearly straight. Apex approximately central, blunt; anterior slope steep; lateral slopes about as steep as anterior slope, but posterior slope gentle. Surface irregular.

Interior with low median ridge rising to a sharp point at the valve middle; anterior adductor scars narrowly elliptical, obliquely placed and forming low ridges which, with the median ridge, divide the valve into three parts; posterior adductor scars large, but lightly impressed. Anterior half with strong pallial ridges.

Measurements in mm.—Length, 10.6; maximum width, 14.0; height, 3.4.

Types.—Holotype U.S.N.M. No. 124192.

Horizon and locality.—Mural limestone, from a small hill 300 yards east of U. S. Highway 80, NW $\frac{1}{4}$ SW $\frac{1}{4}$ NE $\frac{1}{4}$ sec. 36, T. 23 S., R. 25 E., Bisbee Quadrangle, Arizona.

Discussion.—This genus has not hitherto been identified among North American fossils. The laterally elongated muscle scars and short median septum are characteristic. The species is like *Cramiscus suessi* (Bosquet) from the Maastrichtian of Holland in having the apex near the middle and a long, flat posterior slope, but the Dutch species is more swollen anteriorly and is a much deeper shell.

CYCLOTHYRIS AMERICANA Cooper, new species

Plate 1A, figures 1-17

Shell of about medium size for the genus, subtriangular in outline; maximum width at or near the middle; valves subequal in depth, the brachial valve having a slightly greater depth; anterior commissure gently uniplicate; surface costellate, costellae numbering about 32 to 42 along the anterior margin.

Pedicle valve moderately convex in lateral profile, with the maximum convexity near the middle; beak apiculate, nearly straight to sub-erect, making an angle of 60° to 80°. Umbo swollen; beak ridges moderately strong and defining a fairly broad, gently concave inter-area; sulcus originating in the anterior third to half, shallow and occupying about one-third the width. Flanks gently convex, descending steeply to the sides. Deltidial plates conjunct, auriculate; foramen submesothyrid, oval in outline.

Pedicle valve interior with strong but small teeth; dental plates stout and fairly long, not surrounding the muscle field which is large and broadly elliptical; diductor scars subreniform in outline; adductor scars posterior to diductors; no pedicle collar.

Brachial valve strongly convex in lateral and anterior profiles; umbo swollen; fold low or defined only as a wave of the commissure; flanks convex; posterolateral slopes steep. Brachial valve interior with long, slitlike sockets bounded by moderately strong socket ridges; hinge plate divided; crura curved, short, of radulifer type.

MEASUREMENTS IN MILLIMETERS

	Length	Width	Thickness
Holotype U.S.N.M. No. 124193a.....	14.0	13.6	9.0
Paratype U.S.N.M. No. 124193b.....	11.8	12.0	9.0

Types.—Holotype U.S.N.M. No. 124193a; figured paratypes U.S.N.M. Nos. 124186a-e; measured paratype U.S.N.M. No. 124193b.

Horizon and locality.—Mural limestone, from a small hill 300 yards east of U. S. Highway 80, NW $\frac{1}{4}$ SW $\frac{1}{4}$ NE $\frac{1}{4}$ sec. 36, T. 23 S., R. 25 E., Bisbee Quadrangle, Arizona.

Discussion.—This species is characterized by its moderate size, convex valves and costellate surface. One of the significant features of the Arizona species is the poor development of the fold and sulcus, which is strongly developed only at the front. A few specimens of rhynchonellids have been found in the American Lower Cretaceous which are probably referable to *Cyclothyris*. None of these resembles the present species. The National Museum has a specimen of *Cyclothyris* from the Main Street formation, Fort Worth, Tex., but it is transversely elliptical rather than strongly triangular as the Mural species is. Of three specimens of *Cyclothyris* from the Edwards limestone, Presidio County, Texas, two are strongly transverse, but the third is suggestive of *C. americana*.

The British species most suggestive of *C. americana* is *C. nuciformis* (Sowerby), but this differs in having a pronounced fold and sulcus for at least half the valve length. Some young specimens from the Cretaceous of France called *Cyclothyris compressa* (Lamarck) or *C. depressa* (Sowerby) suggest the American species but they are usually more transverse or are demonstrable aberrations of a variable species.

CYCLOTHYRIS species

A single specimen (U.S.N.M. No. 124216) differing importantly from *C. americana* was found with the other specimens described herein. Although somewhat crushed, it differs from *C. americana* in being much wider and in having a fairly prominent fold and sulcus that originate a short distance anterior to the middle.

RECTITHYRIS VESPERTINA Cooper, new species

Plate 1B, figures 18-37

Shell small for the genus, elongate oval in outline and with the maximum width at the middle; sides gently rounded; anterior margin narrowly rounded. Valves unequal in depth, the pedicle valve having the greater depth. Posterior margin narrowly rounded to subcarinate; anterior commissure rectimarginate to faintly uniplicate; lateral commissure nearly straight. Surface smooth except for concentric lines and varices of growth.

Pedicle valve moderately convex in lateral profile and with the maximum convexity at about the middle; anterior profile fairly strongly convex; umbonal region narrowly convex to subcarinate, the narrow swelling continued nearly to the median region where it dies out. Anterior third flattened to faintly sulcate. Beak erect, obliquely truncated; foramen broadly elongate, moderately large, oval to circular, submesothyrid to mesothyrid. Deltidial plates conjunct, not covered by beak, suture visible. Beak ridges strong.

Interior of pedicle valve with large and thick teeth; dental plates obsolete; pedicle collar small. Muscle marks too indistinct to discern individual scars or pattern of field.

Brachial valve shallow, gently convex in lateral profile and broadly convex in anterior profile; umbonal region gently swollen; beak obscured by the overlapping of the deltidial plates; median region gently swollen and forming a barely perceptible fold which appears at the front margin as a gentle wave of the commissure in the direction of the brachial valve; flanks gently inflated and with short, steep sides.

Interior with short stout loop having short crura and short blunt crural processes; descending lamellae short; transverse ribbon broad in adults, fairly strongly elevated and with a flattened crest at its middle; outer socket plate moderately broad, moderately concave; inner socket plates nonexistent to small; inner socket ridge strong, overlapping the teeth. Cardinal process small, wide and short. Musculature and pallial marks poorly impressed, elongate, somewhat tear-shaped.

MEASUREMENTS IN MILLIMETERS

		Length	Brachial length	Width	Thickness
Holotype	U.S.N.M. No. 124194b.....	17.6	14.0	14.0	9.4
Paratype	U.S.N.M. No. 124194a.....	16.9	13.9	12.5	8.8
"	" " 124194c.....	20.3	17.4	17.4	11.6
"	" " 124194d.....	5.4	4.7	3.9	2.7
"	" " 124194e.....	11.4	9.2	8.9	5.2

Types.—Holotype U.S.N.M. No. 124194b; figured paratypes U.S.N.M. Nos. 124187, 124188, 124194c, d, 124195, 124195a, 124196c; unfigured paratypes U.S.N.M. Nos. 124194a, e, 124196a, b, 124205, 124218.

Discussion.—This species is characterized by the unequal convexity of the valves, the suberect to erect beak (Thomson classification, 1927), rectimarginate to faintly plicate anterior commissure, and short, stout loop. I am not completely happy about the assignment of this

species to *Rectithyris* but this appears to be the only genus at present to which it can be assigned. Points of agreement with *Rectithyris* as defined by Sahní (1929) appear: the mesothyrid foramen, the easily visible deltidial plate, rudimentary cardinal process, the inner hinge plates, even though they are not strongly developed, and the constriction of the broad transverse ribbon to form a median, flattened crest. Deviations from *Rectithyris* are the curvature of the beak, less strongly triangular loop, and smaller foramen.

Some points of similarity exist between the Arizona species and *Neoliothyridina*. The loop of the latter is like that of *R. vespertina* and according to Sahní's figures (1929, pl. 9, figs. 19, 20) shows the same type of variation. The loop shown in figure 20 has nearly parallel sides and the crural processes are well anterior to the crural bases, whereas the loop shown in figure 19 has the crural processes located almost at the junction of the crura and the crural bases. The beak characters and other details of *Neoliothyridina*, however, are too different to permit use of that name.

No known species of *Rectithyris* is like this American species; consequently, no direct comparison is possible.

Variation of the loop.—Variations in parts of the loop are evident in many of the specimens, but these variations could not be correlated with shape or shell differences. In some specimens the brachial valve is distinctly flatter than in others, but this difference did not accord with loop differences. In the young, loop variation is evident in the length of the descending branch anterior to the crural base. One specimen, paratype U.S.N.M. No. 124196a, has the crural process given off almost at the junction of the descending branch with the crural base. In another, plate 1B, figure 33, the crural process is located a short distance anterior to the crural base. In this specimen the crural base appears as a ridge bounding the inner socket plate. This is true of a somewhat larger and more-elongate specimen shown in figures 29-31 on the same plate. This is not true, however, of the largest and oldest loop figured, same plate, figures 34 and 35, in which the descending process is short and the posterior extension of the crural base is buried in the formation of modest inner hinge plates. The presence of inner hinge plates appears to be an age character, at least in this case.

Abnormal specimen.—This species shows considerable variation in exterior as well as interior features. Such variability is to be expected, but the occurrence of a freak specimen having the crural processes united is unusual. This specimen is paratype U.S.N.M. No. 124195a. The beak is broken and most of the brachial valve broke from the

specimen during the etching and was not recovered. Unfortunately the loop is thus revealed from the dorsal side which is not the most advantageous view for appreciation of the structure.

The loop is of the normal size as shown by other specimens. The descending branch is very stout and the transverse band is strong and thick. The crural processes appear to have been normal but the points grew inward and united to form a transverse band, thinner than the anterior one but with the band convex toward the pedicle valve and having a form like that of the normal ribbon.

GEMMARCULA ARIZONENSIS Cooper, new species

Plate 2A, figures 1-28; plate 4B, figures 3-6

Shell small, attaining a width of slightly more than one-half inch, transversely elliptical in outline; wider than long and with a narrow hinge. Widest at about the middle. Sides rounded; anterior margin subnasute to broadly rounded; anterior commissure rectimarginate to faintly uniplicate, the uniplication clearly visible only in old specimens. Valves unequal in depth, the pedicle valve having the greater depth. Surface multicostate, the costae appearing in three generations. Costae numbering 20 to 24 on the front margin of an average adult.

Pedicle valve moderately to strongly convex in lateral profile and broadly to strongly convex in anterior profile, the convexity in both profiles depending upon age. Umbo somewhat narrowly convex, the convexity continued anteriorly as an indistinct fold which is bounded somewhat indistinctly by two costae stronger than those surrounding them; median region swollen; flanks and anterior slope steep. Beak irregular from pedicle pressure against rough surface; interarea wide and long; foramen large and circular; deltidial plates disjunct in the young, conjunct in old specimens and forming a symphytium.

Interior of the pedicle valve with short but stout dental plates, strong transverse teeth; callosity of pedicle collar on floor of delthyrial cavity thick; median septum low, extending anteriorly to beyond the valve middle.

Brachial valve gently to moderately convex in lateral profile, broadly but gently convex in anterior profile; umbo gently convex, often abraded by pedicle pressure against the substratum. Fold barely perceptible except in old specimens, and usually defined by a median crowding and smaller size of the costellae. Flanks gently swollen and with long, gentle slopes to the margins.

Interior of the brachial valve with a thick concave notothyrial callosity buttressed by a strong median septum that extends to about the

valve middle; plates bounding sockets broad; outer socket ridges broad; sockets long and deep. Crura short; crural processes short and pointed; loop having form of early dallinid development, braced at its junction with the septum by a wide plate concave toward the anterior; descending branches slender; ascending branches broad; transverse ribbon broad and with two prongs on each side which are directed toward the pedicle valve. Hinge plate usually obscured by callus which smooths the notothyrial region; cardinal process a wide, bilobed thickening on the posterior margin of the notothyrial platform formed by the callus covering the hinge plate.

Development of the loop.—The smallest specimens showing interior details are 2.0 mm. wide (paratype U.S.N.M. No. 124200a) and 2.7 mm. (paratype U.S.N.M. 124198a). In these specimens the septum is continuous from the hinge platform to the valve middle where it is expanded ventrally toward the pedicle valve to form the pillar. Viewed from the anterior the expanded pillar is divided by a groove and the ventral and dorsal sides diverge slightly from each other, the beginnings of the loop ring. Crural processes and descending branches are either not preserved or not yet formed, probably the former. The notothyrial region is filled with solid callus.

The next larger specimen is 3.6 mm. in width (paratype U.S.N.M. No. 124199). Both valves are preserved. The pedicle valve shows a wide and completely open delthyrium with no trace of the deltidial plates. Thickening on the floor of the delthyrial cavity is strong and the median ridge anterior to this thickening is well developed. Inside the brachial valve the notothyrial region is solid as in the preceding specimen, but the septum is short and high. The crural processes are well developed and the crura are short and thick. The descending lamellae join the lower or dorsad diverging branches of the anterior end of the pillar, the anterodorsal side of which is now more deeply cleft. The ventral portion of the septum is elongated and the two lamellae diverging widely from the pillar are roofed by a flat plate, the pre-campagiform hood of Elliott.

A third specimen of 5 mm. width (paratype U.S.N.M. No. 124201a) also shows the median septum and its anterior expansion. This specimen differs from the preceding one in having a definite concavity in the notothyrial callus, bounded by the crural bases. Other details of the loop can only be inferred.

A fourth specimen 5.7 mm. in width (paratype U.S.N.M. No. 124198b) shows additional details of the loop, but part must be inferred from ridges and remnants. The notothyrial callosity is thick and is buttressed by a strong median septum. The crura are very short

and the descending lamellae are moderately broad and extend from the crural processes anteriorly to join the median part of the curved lateral plates at the distal end of the septum. The incision at the anterior end is much deepened and the anterior ends of the broken loop ring are beginning to diverge widely.

No specimens between 6 and 12 mm. preserving good details of the loop were taken from the acid residues. Specimens 12 mm. wide or wider evidently have adult loops, but none of them are complete. The lateral branches connecting the septum to the loop are broad, stout, and long, frequently being strengthened by a median triangular plate. The loop of an adult specimen 16.5 mm. wide (paratype U.S.N.M. No. 124220) has a broad transverse ribbon with long ears.

MEASUREMENTS IN MILLIMETERS

	Length	Brachial length	Mid-width	Hinge width	Thickness
Holotype U.S.N.M. No. 124197a..	10.1	8.8	12.3	8.7	5.2
Paratype U.S.N.M. No. 124197b..	13.1	11.1	13.5	10.4	8.7
“ “ “ 124206a..	12.2	9.6	14.0	10.8	6.5
“ “ “ 124206b..	13.4	10.6	14.0	10.7	7.6
“ “ “ 124206c..	11.5	9.0	13.0	10.9	6.4
“ “ “ 124206d..	7.2	5.3	7.5	?	4.2
“ “ “ 124206e..	5.1	4.3	5.8	5.9	2.6

Types.—Holotype U.S.N.M. No. 124197a; figured paratypes U.S.N.M. Nos. 124197b, d-j, 124198a, b, 124199, 124201a, b, 124220; measured paratypes U.S.N.M. Nos. 124206 a-e; unfigured paratypes U.S.N.M. Nos. 124197c, 124200a, b.

Horizon and locality.—Mural limestone, from a small hill 300 yards east of U. S. Highway 80, NW $\frac{1}{4}$ SW $\frac{1}{4}$ NE $\frac{1}{4}$ sec. 36, T. 23 S., R. 25 E., Bisbee Quadrangle, Arizona; Rancho Nuevo, 3 miles east of Santa Rosalia, Sonora, Mexico.

Discussion.—This species is characterized by having a low and indistinct fold and sulcus and differs from all other described species of *Gemmarcula* in this respect. This is the first report of the genus in North America. *Gemmarcula arizonensis* is about the same size as *G. aurea*, type species of the genus, and has a cardinal process like it, but the exterior is different as noted above. *Gemmarcula menardi* (Lamarck), a well-known species in France and Great Britain, is larger than the American species and has a much more pronounced fold and sulcus. It also differs from the Arizona shell in having a more elaborate cardinal process.

GEMMARCULA MENARDI (Lamarck)

Plate 2B, figures 29-34

Figures of the interior and exterior of this fine species are introduced for comparison with *G. arizonensis*. Note elaborate development of the cardinal process in this European species.

Horizon and locality.—Cretaceous (Green Sand), LeMans, Sarthe, France.

PSILOTHYRIS Cooper, new genus

Generally small to medium size, oval to subpentagonal in outline; anterior commissure rectimarginate to uniplicate; valves unequally convex, the pedicle having the greater depth and convexity.

Pedicle valve with strong beak ridges; beak erect; foramen round, small to large, submesothyrid to mesothyrid; deltidial plates disjunct to conjunct, often worn away by pedicle pressure. Interior with stout, thick teeth, buttressed by stout dental plates; no pedicle collar; muscle scars not discernible in available material.

Cardinalia small; hinge plate undivided, short, often upturned on its anterior edge; inner socket plate concave, stout; crura short, stout; crural process long and slender; loop simple, long dalliniform, forming a broad ribbon and having a broad transverse band in the adult; median septum of the adult short, slender, and may or may not buttress the hinge plate, and reduced to a faint myophragm at the valve middle. Young stages with loop metamorphosis like that of the Dallinidae.

Type species.—*Psilothyris occidentalis* Cooper, new species.

Discussion.—This species is characterized by its smooth exterior, simple uniplicate folding, short inner hinge plate and long dalliniform loop. Details of the formation of the hinge plate and the development of the loop are discussed under the specific description. The combination of characters exhibited by *Psilothyris* is different from any described Cretaceous dallinoid and is also unlike any described smooth Jurassic zeilleroid and dallinoid.

Of smooth Jurassic zeilleroids that resemble *Psilothyris* more or less closely, *Zeilleria*, *Microthyridina*, *Rugitela*, and *Ornithella* are provided with a strong median septum in the brachial valve and the folding of all of them is different from that of *Psilothyris*. *Aulacothyris* and *Antiptychina* are differently folded, these two genera having a strongly sulcate brachial valve. The dallinoids *Plesiothyris* and *Obovothyris* have long septa and different folding. *Epicyrta* has a carinate brachial valve and is thus quite different externally.

This genus, although not named until now, was recognized by Deslongchamps (1884, p. 189) in his discussion of the genus *Zeilleria*. He characterizes the division as having a relatively short, thick beak having a very large foramen. The shell is globular, short, and compact. It is unique in the Cretaceous.

PSILOTHYRIS OCCIDENTALIS Cooper, new species

Plate 3B, figures 4-24; plate 4A, figures 1, 2

Shell small, attaining a length of five-eighths inch; outline sub-pentagonal with the length slightly greater than the width; greatest width located slightly posterior to the middle; sides sloping medially; anterior margin subtruncate; posterior margin forming an obtuse angle. Anterior commissure uniplicate; lateral commissure straight. Valves unequal in depth, the pedicle valve deeper; surface smooth except for concentric lines and varices of growth.

Pedicle valve strongly convex in lateral profile, with the maximum convexity slightly posterior to the middle; anterior profile strongly convex; umbonal region inflated; beak small, erect; beak ridges strong. Median region swollen; anterior slope flattened; flanks swollen and steep. Foramen small, round, mesothyrid, slightly labiate. Deltidial plates conjunct, suture visible. Interior of pedicle valve with large teeth supported by stout dental plates. No pedicle collar. Muscle marks lightly impressed.

Brachial valve in lateral profile flattened in the median region but convex at the posterior and anterior; anterior profile broadly and gently convex. Umbonal region swollen but median area flattened; flanks narrowly convex.

Interior of the brachial valve with short, undivided hinge plate deeply excavated anteriorly and thickened, elevated or puckered on the anterior edge. Socket ridge short, stout. Crura short; crural processes long and slender in the adult loop but short and blunt in the young. Loop long and free in the adult; loop short, broad, and attached to a short septum on the floor of the valve in the young. Septum in the adult short and confined to a position at the beak and under the hinge plate and may or may not support the hinge plate.

Development of the loop.—In the smallest specimen available, measuring 3 mm. in length and probably the same in width (paratype U.S.N.M. No. 124190k), the notothyrial region is deeply concave and without a hinge plate. The crura are slender and arise from ridges bordering the notothyrial cavity. The descending lamellae are short and their anterior ends converge to unite with a septal blade or pillar

that springs from the floor of the valve near the middle. This pillar is much expanded longitudinally with free edges extending a short distance posteriorly, but also anteriorly to a point about three-fourths the length of the valve from the beak. The anterior extension appears to be a long, broad-ribbed ring. The details cannot be ascertained because this part of the structure is obscured by silicious material. This is the pre-campagiform stage.

Details of the cardinalia are clear in a specimen without loop measuring 4.2 mm. in length (paratype U.S.N.M. No. 124202d). The floor of the notothyrium is thickened by ridges joining the crural bases and the septum is now extended posteriorly to meet the center of these lateral ridges (pl. 3B, fig. 13). The expanded anterior end of the septum is free, but no other details are available.

A specimen measuring 4.5 mm. in diameter (paratype U.S.N.M. No. 124202g) is somewhat more advanced than the previous one. The notothyrial cavity is now deeply concave, the lateral extensions thickened and anteriorly excavated to simulate a hinge plate supported by the median septum. The crural processes on the loop are well developed and are located just anterior to the hinge plate. The descending branches of the loop attach to the distal expanded end of the septum near its dorsal extremity. The greatest change has taken place at the free part of the septum, the anterior end of which is distinctly divided by an incision in its anterior end and the remains of a ring mounting the ventral edge is clearly visible. This is probably the frenuliniform stage of development.

A still more advanced stage, the terebrataliform stage, is shown by a specimen 6.6 mm. in diameter (paratype U.S.N.M. No. 124202i). The hinge plate is still deeply concave and the crural processes moderately long. The septum is well developed and high but does not now reach to the middle. The descending branches of the loop are broad and are now extended far anterior to the end of the septum. The loop is nevertheless still attached to the distal end of the septum by two short branches, but the septum does not extend anterior to its point of contact (plate 3B, figure 17). The specimen does not preserve a ring or ascending branch, but remnants of it are visible.

The next specimen of the series is 7.6 mm. in length and slightly less in width (paratype U.S.N.M. No. 124190h). The hinge plate has become considerably shallower by anterad growth of a transverse plate at its anterior end; the crural processes are large and the branch between them and the hinge plate is now nearly obsolete. The descending branches are free of the septum, but projections, which face inward and represent the remnant of the septal attachments, appear at

about their middle. The septum has been absorbed to a mere remnant which extends for a short distance only anterior to the hinge plate. Except for the incompletely developed hinge plate and the remnants of the septal attachments, the loop is essentially adult in character. This stage is the dalliniiform stage.

By summarizing the evidence from these few specimens it is possible to give a fairly complete account of the loop development. Prior to 3 mm. the median septum must show as a small projection from the floor. At 3 mm. the septum has become elongated and the descending branches have grown anteriorly to meet the sides of the elongated free distal expanded part of the septum and the ring bud starts to develop. By 4½ mm. the expanded end of the septum splits laterally and the ring enlarges, the septum having a deep reëntrant anteriorly and the descending branches extended a considerable distance anteriorly. At 6.6 mm. the loop is strong, with broad descending branches extended beyond the anterior end of the septum, and the loop attachment to the septum is a small process. At 7.6 mm. the loop is now free of the septum which has become nearly completely resorbed except for the short remnant supporting the hinge plate. Remnants of the process attaching the loop to the septum can be seen in specimens having attained a length of 12.5 millimeters.

The hinge plate is deeply concave in the young, but in the 7.6 mm. stage the transverse plate forming the flat and undivided hinge plate forms, and this lengthens with advancing age. In old age it becomes puckered or upturned on its free edge.

MEASUREMENTS IN MILLIMETERS

		Length	Brachial length	Width	Thickness
Holotype	U.S.N.M. No. 124191.....	15.1	12.4	13.9	9.7
Paratype	U.S.N.M. No. 124189.....	13.3	11.0	12.2	8.1
"	" " 124190a.....	11.4	9.6	10.7	6.0
"	" " 124190b.....	12.4	10.4	11.7	7.5

Types.—Holotype U.S.N.M. No. 124191; figured paratypes U.S.N.M. Nos. 124190a, c, e, f, h-j, 124202a, d-i; measured paratypes U.S.N.M. Nos. 124189, 124190a, b; described but unfigured paratypes U.S.N.M. No. 124190k; unfigured paratypes U.S.N.M. Nos. 124190d, g, 124202b.

Horizon and locality.—Mural limestone, from a small hill 300 yards east of U. S. Highway 80, NW¼SW¼NE¼ sec. 36, T. 23 S.,

R. 25 E., Bisbee Quadrangle, Cochise County, Arizona; Rancho Nuevo, 3 miles east of Santa Rosalia, Sonora, Mexico.

Discussion.—This species is characterized by its compact form, small foramen, moderately strongly uniplicate commissure, flatly convex brachial valve and deep pedicle valve. No other species of this genus is now known in North America to which this one can be compared. The species most like *P. occidentalis* outside of North America is "*Waldheimia*" *tamarindus* (Sowerby) from the British Isles. A variety of forms now appears under this name in the British Isles, but specimens of *P. tamarinda* from Faringdon, England, are most like the American species. They differ, however, in having a narrower anterior region, a larger foramen and much less convex pedicle valve. The development of the median septum in the interior of both the British and American forms is very slight.

PSILOTHYRIS TAMARINDA (Sowerby)

Plate 3C, figure 25

The interior of a brachial valve is introduced for comparison with *P. occidentalis*. Note the low and reduced median septum and the short undivided hinge plate.

Horizon and locality.—Cretaceous (Aptian—Lower Green Sand), Faringdon, Berkshire, England.

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PLATE 2

- A. *Gemmarcula arizonensis* Cooper, new species..... 7
- 1-5, Anterior, posterior, side, brachial, and pedicle views, respectively, of a complete specimen, $\times 1$, paratype U.S.N.M. No. 124197b. 6-10, Brachial, side, posterior, anterior, and pedicle views, respectively, $\times 2$, of holotype U.S.N.M. No. 124197a. 11, Complete specimen tilted to show interarea and deltidium (= united deltidial plates), $\times 3$, paratype U.S.N.M. No. 124197d. 12, View of the interarea and disjunct deltidial plates of a young specimen, $\times 3$, paratype U.S.N.M. No. 124197g. 13, Posterior part of a pedicle valve tilted to show callosity on floor of delthyrial cavity, low median septum, and discrete deltidial plates, $\times 2$, paratype U.S.N.M. No. 124197h. 14, Immature pedicle valve, $\times 4$, showing deltidial plates just forming and callosity on floor of delthyrial cavity, paratype U.S.N.M. No. 124201a. 15, Interior of an incomplete brachial valve, $\times 3$, paratype U.S.N.M. No. 124197e, showing cardinalia. 16, Interior of a brachial valve younger than the preceding, $\times 4$, showing cardinalia, paratype U.S.N.M. No. 124197f. 17, Interior of an old specimen showing deeply excavated notothyrial callosity simulating a concave hinge plate, crura and crural processes, $\times 3$, paratype U.S.N.M. No. 124197i. 18, 19, Tilted and interior views of a young brachial valve showing hooded pre-campagiform stage of loop, $\times 4$, paratype U.S.N.M. No. 124199. 20, Interior of the pedicle valve of the preceding specimen, with open delthyrium, $\times 4$. 21, A young specimen, $\times 4$, showing beginning of ring and attachments of descending lamellae of loop, paratype U.S.N.M. No. 124198a. 22, A still larger specimen than the preceding showing deeper cleft in remnant of ring, $\times 4$, paratype U.S.N.M. No. 124198b. 23, Young brachial valve tilted to show cleft in loop ring, $\times 4$, opposite to pedicle valve shown in figure 14, paratype U.S.N.M. No. 124201b. 24, Specimen with pedicle valve partially removed to show attachment of loop to septum and long anterior branches of the descending lamellae, $\times 2$, paratype U.S.N.M. No. 124197j. Mural limestone, from a small hill 300 yards east of U. S. Highway 80, NW $\frac{1}{4}$ SW $\frac{1}{4}$ -NE $\frac{1}{4}$ sec. 36, T. 23 S., R. 25 E., Bisbee Quadrangle, Cochise County, Arizona.

Page

25-28, Interior, posterior, side tilted, and interior posteriorly tilted views, respectively, of an adult specimen showing terebrataliform loop, $\times 2$, paratype U.S.N.M. No. 124220. Mural limestone, Rancho Nuevo, 3 miles east of Santa Rosalia, Sonora, Mexico.

- B. *Gemmarcula menardi* (Lamarck)..... 10
 29, 30, Brachial and side views of a complete specimen, $\times 1$, for comparison with *Gemmarcula arizonensis*, hypotype U.S.N.M. No. 124223c. 31, Interarea of the pedicle valve, $\times 2$, showing symphytium (or deltidium), teeth, and foramen, hypotype U.S.N.M. No. 124223a. 32, 33, Interior and posterior views of the brachial valve showing complicated cardinal process, $\times 2$, hypotype U.S.N.M. No. 124223b. 34, Brachial interior showing part of loop, $\times 2$, for comparison with *G. arizonensis*, counterpart of pedicle valve shown by figure 31. Cretaceous (Green Sand), Le Mans, Sarthe, France.

PLATE 3

- A. *Craniscus hesperius* Cooper, new species..... 2
 1, 2, Brachial and side views, $\times 1$, of holotype U.S.N.M. No. 124192. 3, Interior of the preceding, $\times 2$, showing transverse muscle scars. Mural limestone, from a small hill 300 yards east of U. S. Highway 80, NW $\frac{1}{4}$ SW $\frac{1}{4}$ NE $\frac{1}{4}$ sec. 36, T. 23 S., R. 25 E., Bisbee Quadrangle, Cochise County, Arizona.
- B. *Psilothyris occidentalis* Cooper, new species..... 11
 4-8, Anterior, posterior, side, brachial, and pedicle views, respectively, $\times 2$, of holotype U.S.N.M. No. 124191. 9, 10, Brachial and anterior views of another individual, showing uniplicate anterior commissure, $\times 1$, paratype U.S.N.M. No. 124190a. 11, Side view of a specimen broken to show descending branches of the long dalliniform loop and part of the wide ascending branch, $\times 2$, paratype U.S.N.M. No. 124202a. 12, Interior of the pedicle valve showing deltidium (united deltidial plates), submesothryrid foramen, and teeth, paratype U.S.N.M. No. 124190c. 13, 14, Two small specimens in pre-campagiform stage, $\times 4$, showing the median septum and pillar of an early juvenile stage, paratypes U.S.N.M. No. 124202e, d. 15, Another juvenile specimen in the same stage as the preceding showing part of descending branch attached to pillar, $\times 4$, paratype U.S.N.M. No. 124202h. 16, Another juvenile specimen, probably in frenuliform stage, tilted slightly to the side and showing descending branches attached to pillar and part of loop ring, $\times 4$, paratype U.S.N.M. No. 124202g. 17, Immature specimen in terebrataliform stage showing descending branches of loop attached to median septum and the deep cleft at the anterior of the loop, $\times 4$, paratype U.S.N.M. No. 124202i. 18, A specimen older than the preceding and in the dalliniform stage showing receded median septum but remnants of processes of attachment on the descending branches

of the loop, $\times 4$, paratype U.S.N.M. No. 124202f. 19, A slightly larger specimen than the preceding in dalliniform stage showing descending branches and remnantal septal attachments, $\times 4$, paratype U.S.N.M. No. 124190h. 20, Fragment of brachial valve showing hinge plate, sockets, and socket ridges, $\times 4$, paratype U.S.N.M. No. 124190j. 21, Interior of another brachial valve, $\times 4$, showing adductor scars indistinctly, paratype U.S.N.M. No. 124190e. 22, Cardinalia of an adult brachial valve, $\times 4$, showing crural processes and hinge plate with upturned edge, paratype U.S.N.M. No. 124190i. 23, 24, Two views, $\times 4$, of the interior of an adult brachial valve, one (23) tilted and the other not, showing hinge plate socket ridges, almost obsolete median septum, and also the dental plates of the pedicle valve, paratype U.S.N.M. No. 124190f. Horizon and locality same as above.

- C. *Psilothyris tamarinda* (Sowerby)..... 14
 25, Interior of the brachial valve showing cardinalia and nearly obsolete median septum, $\times 3$, figured specimen U.S.N.M. No. 128222. Cretaceous (Aptian—Lower Green Sand), Faringdon, Berkshire, England.

PLATE 4

- A. *Psilothyris occidentalis* Cooper, new species..... 11
 1, 2, Side and interior tilted views of a specimen in pre-campagiform stage 4.5 mm. long showing the pillar before growth of median septum, and descending lamellae, about $\times 14$ and $\times 10$, respectively, paratype U.S.N.M. No. 124202g. Mural limestone, a small hill 300 yards east of U. S. Highway 80, NW $\frac{1}{4}$ -SW $\frac{1}{4}$ NE $\frac{1}{4}$ sec. 36, T. 23 S., R. 25 E., Bisbee Quadrangle, Cochise County, Arizona.
- B. *Gemmarcula arizonensis* Cooper, new species..... 7
 3, 4, Interior and side views of a brachial valve 3.6 mm. wide showing remnants of pre-campagiform hood, pillar, and beginning of loop ring, about $\times 17$, paratype U.S.N.M. No. 124199.
 5, 6, Side and interior views of brachial valve showing the adult loop, about $\times 4.5$, paratype U.S.N.M. No. 124220. Horizon and locality same as in text; (3) and (4) from Arizona, (5) and (6) from Sonora, Mexico.

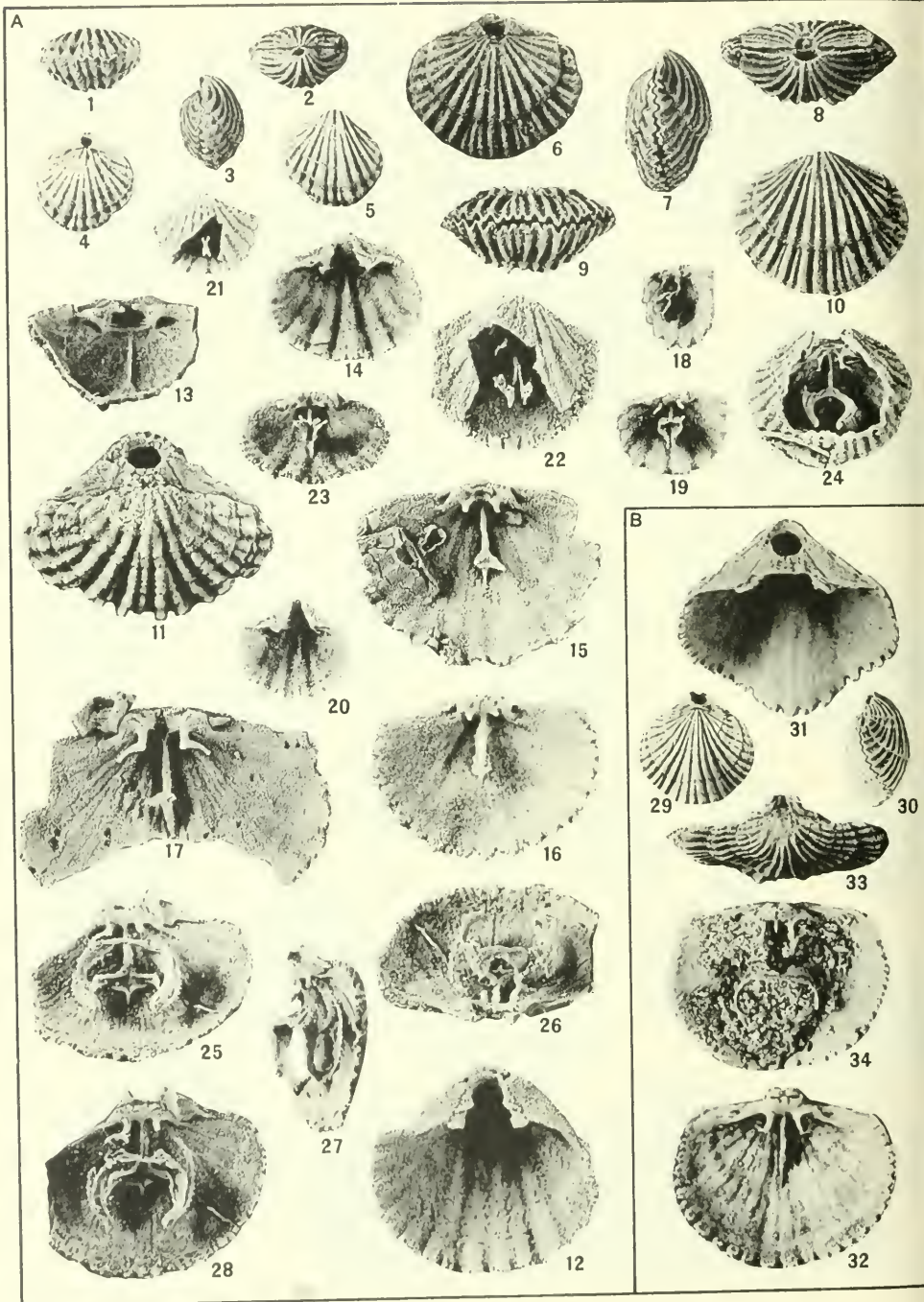
Abbreviations

ab = ascending branch of loop	g = groove of pillar
cb = crural base	p = septal pillar
cp = cardinal process	pf = remnant of pre-campagiform flange
dl = descending branch of loop	s = septum
e = ear of loop	sdl = scar of broken descending lamella

(Drawings by Lawrence B. Isham.)

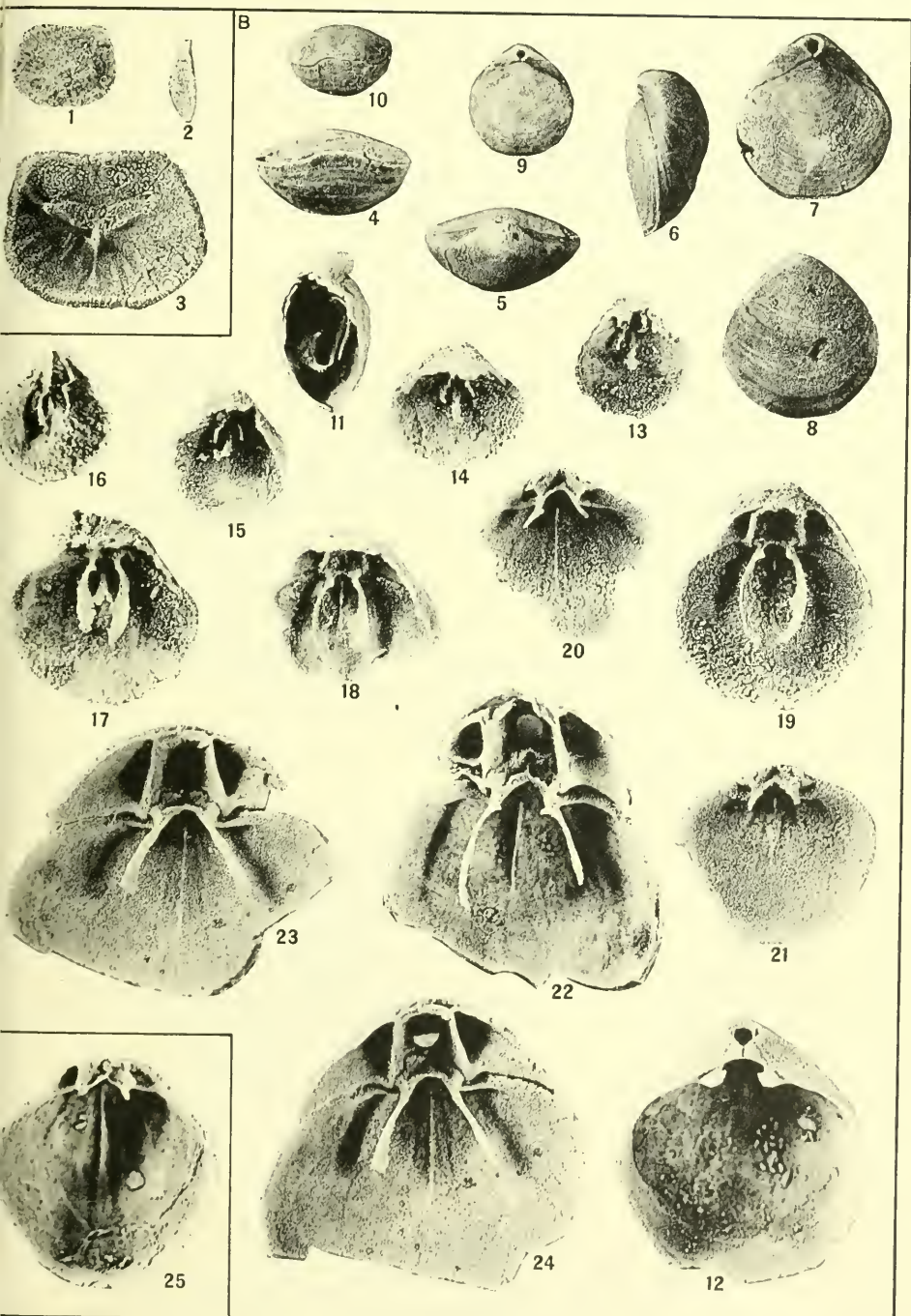


CYCLOTHYRIS AND RECTITHYRIS
(SEE EXPLANATION AT END OF TEXT.)

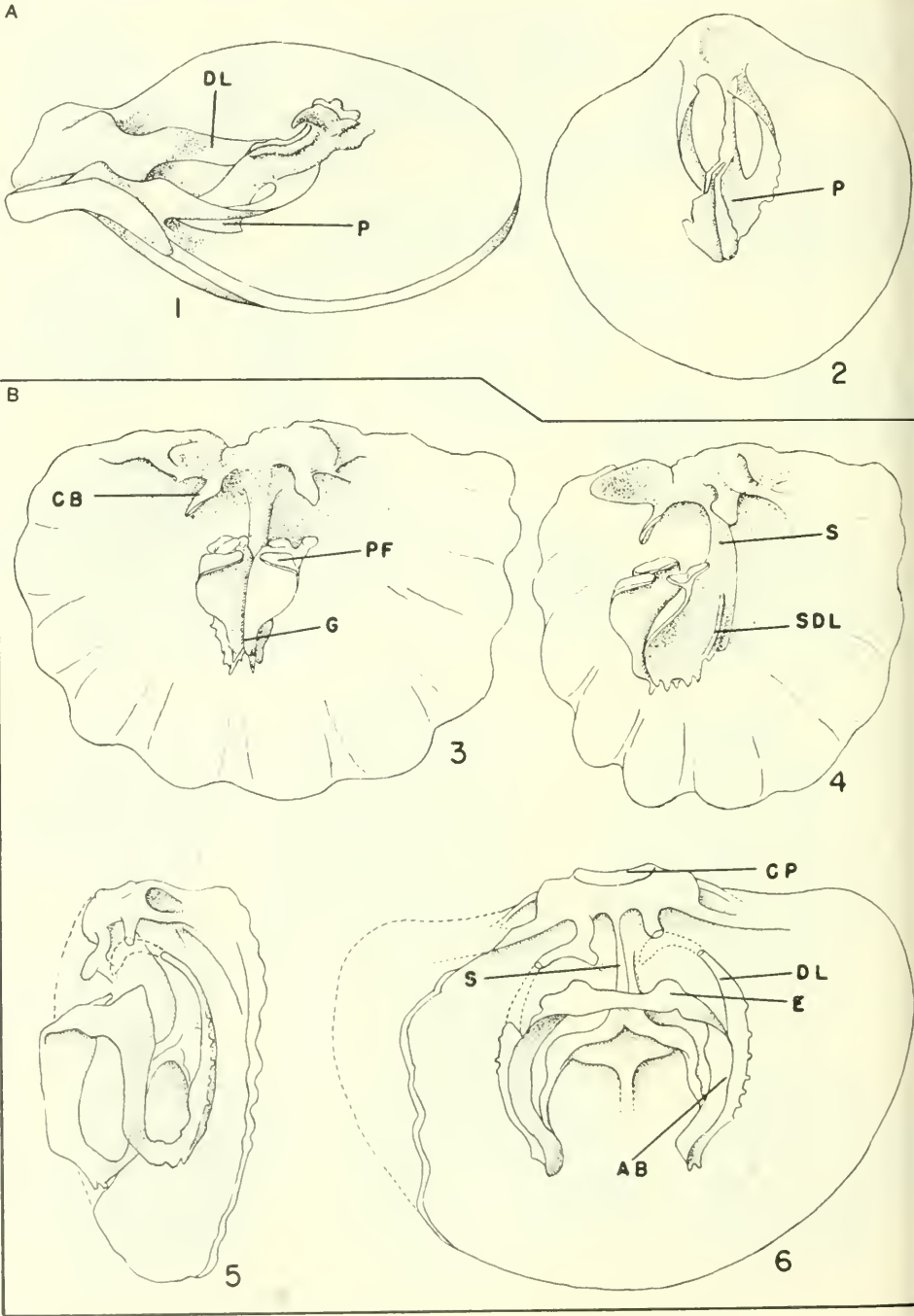


GEMMARCULA

(SEE EXPLANATION AT END OF TEXT.)



CRANISCUS AND PSILOTHYRIS
(SEE EXPLANATION AT END OF TEXT.)



PSILOTHYRIS AND GEMMARCULA
(SEE EXPLANATION AT END OF TEXT.)

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A CHECK-LIST OF THE FOSSIL AND
PREHISTORIC BIRDS OF NORTH
AMERICA AND THE
WEST INDIES

By

ALEXANDER WETMORE

Research Associate, Smithsonian Institution



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**A CHECK-LIST OF THE FOSSIL AND PRE-
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The present check-list is an amplification of the one published in the Smithsonian Miscellaneous Collections in 1940 (vol. 99, No. 4) and is complete to November 1955 so far as records have come to attention. To the present time these check-lists have covered the area of the check-list of living birds of the American Ornithologists' Union, namely North America north of México, with the addition of Baja California. It has seemed desirable now to include also the records, comparatively few in number, for México and the West Indies, since this information is complementary and otherwise is available only in widely scattered sources. Various of these latter records are of species of birds described from bones found during archeological excavations in Indian kitchen middens of pre-Columbian age or during the exploration of caverns. The species concerned have long been extinct, so that the only knowledge regarding them is embodied in their skeletal remains. No living examples have been known. It is useful therefore to include them for reference with other species of fossil status, since they do not figure in check-lists of existing birds and since possibly they may be encountered at some future time in true fossil form. They have the same pertinence therefore as species described from Pleistocene beds whose bones have been found subsequently in Recent deposits.

The considerable amount of information now available has allowed more detail relative to geological formations from which the various records have come, and these data have been brought down to date as far as practicable. In this I have had the advice in certain cases of Druid Wilson, of the U. S. Geological Survey, and also have profited from discussions with Dr. C. Wythe Cooke of the same service, particularly as to formations of the southeastern United States.

In the records from the Pleistocene there has been sufficient study of the deposits of this age known from the western United States to allow indication of position, as to whether they are considered early or

late, of most of the faunas. The situation in Florida is not so clear. Bone beds at Melbourne and Vero overlie the Anastasia formation, a marine Pleistocene deposit, and therefore are considered late Pleistocene. Apparently a newer find at Haile in Alachua County may be from a similar level. The Seminole Field in Pinellas County also appears to overlie the beds of the west coast of Florida that are considered equivalent to the Anastasia, if not exactly the same formation. However, Pliocene exposures are near at hand so that the sequence, from present knowledge, is not clear-cut as it is at Melbourne. Information relative to the localities at Bradenton, Sarasota, and on the Itchtucknee River is far from definite, and other deposits found in caverns, while evidently Pleistocene, are still more uncertain as to actual relationship within that period. Collecting continues actively in the Florida Pleistocene, and presently there should be accumulated sufficient data on the avifauna to permit a reasonable correlation. In the meantime it has seemed better to list all the Florida records as Pleistocene without attempt to indicate the level. To list Melbourne and Vero alone, for example, as late Pleistocene might be misleading.

Recent investigations of Dr. Joseph T. Gregory (Condor, 1952, pp. 73-88) have changed measurably the time-honored concept in which the species of *Ichthyornis* have been associated with the *Hesperornis* group in a superorder (Odontognathae) of the Neornithes, characterized by the possession of teeth. The skull of *Ichthyornis* always has presented an anomaly in that the teeth were in sockets instead of in grooves as in *Hesperornis*. Further, the mandible, or lower jaw, was unduly large in comparison with the rest of the skull and the body skeleton. Dr. Gregory has shown that the jaws attributed to *Ichthyornis* in reality are reptilian and are those of a small mosasaur.

These conclusions destroy the main reasons for the association of *Ichthyornis* and *Hesperornis* in one superorder, though still leaving *Ichthyornis* apart from birds known from later periods to the present, in the biconcave vertebrae. In preliminary consideration it seemed that it might be desirable in the classification to cancel the category of superorders, but on further consideration it appears useful to emphasize the considerable and definite differences that separate *Hesperornis*, *Ichthyornis*, and the penguins from each other and from other groups of birds. This may be accomplished through a new superorder Ichthyornithes for the order Ichthyornithiformes, leaving *Hesperornis* and those others placed near it in the Odontognathae. This will serve as stated above to call attention to the existing peculiarities of these groups and will give a balanced treatment.

The family Mancallidae is added for the two species of *Mancalla* at present recognized, since resemblance between these and the great auk appears due to convergence. The two west-coast forms differ from other auks in the marked modification of the wing for use as a flipper. The genera *Paloelodus* and *Megapaloelodus* have been placed with the typical flamingos in the Phoenicopteridae, a group to which they are unquestionably related. Dr. Hildegarde Howard recently pointed out their differences in the shorter, heavier metatarsus, nonpneumatic femur, and different form in the tibiotarsus and has proposed the family Paloelodidae. To the differences outlined by Dr. Howard there may be added the form of the bill, which, to judge from one incomplete specimen of *Paloelodus ambiguus* Milne Edwards of the Oligocene of western Europe, was gooselike and not bent downward as in the true flamingos. It may be noted also that the toes in *Paloelodus* were definitely longer.

The modern species that occur in the fossil record are distinguished from those not known in living form by the inclusion of a common name in the heading and the statement that the bird is one found in modern form. Most of these are listed under specific scientific names without regard to local race, since most subspecies may not be identified from bones. It is extremely doubtful procedure in most instances to assume that Pleistocene subspecies were the same as those encountered in the region today, and assumption of race is made only where there is reasonable certainty of the identification. The specific names therefore are used in an inclusive sense, though it is evident in wide-ranging groups that two or more subspecies may be covered in the fossil record, for example, in the ruffed grouse, *Bonasa umbellus*, where bones identified as this species are known from such widely separated localities as Maryland and California. This should be understood particularly in cases like that of the raven, *Corvus corax*, or marsh hawk, *Circus cyaneus*, where the range extends to other continents.

The present list gives the record of 189 forms still living, and of 248 species recorded only in an extinct state, this including 11 kinds known only from bones in cave or midden deposits of Recent age. There remain the 12 additional names of uncertain status listed at the end under the heading INCERTAE SEDIS. The increase from the 165 modern forms and 184 extinct species of the list of 1940 is indicative of the growth in knowledge in this field during the comparatively brief interval of 15 years but reveals only part of the increase since many additional records have been found for numerous living species included in 1940.

Class AVES: BIRDS

Subclass NEORNITHES: TRUE BIRDS

Superorder ODONTOGNATHAE: NEW WORLD TOOTHED BIRDS

Order HESPERORNITHIFORMES: HESPERORNITHES

Family HESPERORNITHIDAE: HESPERORNITHES

Genus HESPERORNIS Marsh

Hesperornis MARSII, Amer. Journ. Sci., ser. 3, vol. 3, 1872, p. 360. Type, by monotypy, *Hesperornis regalis* Marsh.

Hesperornis crassipes (MARSH)

Lestornis crassipes MARSII, Amer. Journ. Sci., ser. 3, vol. 11, 1876, p. 509.

Upper Cretaceous (Niobrara formation): Western Kansas.

Hesperornis montana SHUFELDT

Hesperornis montana SHUFELDT, Auk, vol. 32, No. 3, July 1915, p. 293, pl. 18, figs. 4, 6, 8, 10, 12.

Upper Cretaceous (Claggett formation): 1 mile above mouth of Dog Creek, Fergus County, Montana.

Hesperornis regalis MARSII

Hesperornis regalis MARSII, Amer. Journ. Sci., ser. 3, vol. 3, 1872, p. 357.

Upper Cretaceous (Niobrara formation): Smoky Hill River, 20 miles east of Wallace (type locality), and Two Mile Creek, Smoky Hill River, Logan County, Kansas.

Hesperornis gracilis MARSII ¹

Hesperornis gracilis MARSII, Amer. Journ. Sci., ser. 3, vol. 11, 1876, p. 510.

Upper Cretaceous (Niobrara formation): Near Smoky Hill River, western Kansas.

Genus CONIORNIS Marsh ²

Coniornis MARSII, Amer. Journ. Sci., ser. 3, vol. 45, 1893, p. 82. Type, by monotypy, *Coniornis altus* Marsh.

Coniornis altus MARSII

Coniornis altus MARSH, Amer. Journ. Sci., ser. 3, vol. 45, 1893, p. 82, text fig.

Upper Cretaceous (Judith River formation): Dog Creek, Fergus County, Montana.

¹ Gregory, Condor, vol. 54, No. 2, Mar. 26, 1952, p. 74, concludes that the genus *Hargeria*, erected for this species by Lucas, is not separable from *Hesperornis*.

² Shufeldt, Trans. Connecticut Acad. Arts Sci., vol. 19, February 1915, pp. 16, 75, considers this a synonym of *Hesperornis*.

Family BAPTORNITHIDAE³: BAPTORNITHES

Genus BAPTORNIS Marsh

Baptornis MARSH, Amer. Journ. Sci., ser. 3, vol. 14, 1877, p. 86. Type, by monotypy, *Baptornis advenus* Marsh.

Baptornis advenus MARSH

Baptornis advenus MARSH, Amer. Journ. Sci., ser. 3, vol. 14, 1877, p. 86.

Upper Cretaceous (Niobrara formation): Wallace County (type locality), and Butte Creek, Logan County, Kansas.

Superorder ICHTHYORNITHES: ICHTHYORNIS and ALLIES

Order ICHTHYORNITHIFORMES: ICHTHYORNIS and ALLIES

Family ICHTHYORNITHIDAE: ICHTHYORNITHES

Genus ICHTHYORNIS Marsh

Ichthyornis MARSH, Amer. Journ. Sci., ser. 3, vol. 4, November 1872, p. 344. Type, by monotypy, *Ichthyornis dispar* Marsh.

Ichthyornis agilis (MARSH)

Graculavus agilis MARSH, Amer. Journ. Sci., ser. 3, vol. 5, 1873, p. 230.

Upper Cretaceous (Niobrara formation): Butte Creek, Logan County, Kansas.

Ichthyornis anceps (MARSH)

Graculavus anceps MARSH, Amer. Journ. Sci., ser. 3, vol. 3, 1872, p. 364.

Upper Cretaceous (Niobrara formation): North Fork Smoky Hill River, Logan County, about 12 miles east of Wallace, Kansas.

Ichthyornis dispar MARSH

Ichthyornis dispar MARSH, Amer. Journ. Sci., ser. 3, vol. 4, 1872, p. 344.

Upper Cretaceous (Niobrara formation): Near Solomon River, Kansas.

Ichthyornis lentus (MARSH)

Graculavus lentus MARSH, Amer. Journ. Sci., ser. 3, vol. 14, 1877, p. 253.

Upper Cretaceous: Near McKinney, Texas.

³ Lambrecht, Handb. Palaeorn., 1933, pp. 258-260, unites this with the family Enaliornithidae, on what seem insufficient grounds. As suggested by Lucas, Proc. U. S. Nat. Mus., vol. 26, 1903, p. 555, *Baptornis* probably belongs in a distinct order.

Ichthyornis tener MARSH

Ichthyornis tener MARSH, Odontornithes, 1880, pp. 151, 198, pl. 30, fig. 8.

Upper Cretaceous (Niobrara formation): Wallace County, Kansas.

Ichthyornis validus MARSH

Ichthyornis validus MARSH, Odontornithes, 1880, pp. 147, 153, 198, pl. 30, figs. 11-14.

Upper Cretaceous (Niobrara formation): Near Solomon River, Kansas.

Ichthyornis victor MARSH

Ichthyornis victor MARSH, Amer. Journ. Sci., ser. 3, vol. 11, 1876, p. 511.

Upper Cretaceous (Niobrara formation): Wallace County (type locality), and Hackberry Creek, near Smoky Hill River, Gove County, Kansas.

Family APATORNITHIDAE: APATORNITHES

Genus APATORNIS Marsh

Apatornis MARSH, Amer. Journ. Sci., ser. 3, vol. 5, Jan. 21, 1873, p. 162. Type, by monotypy, *Ichthyornis celer* Marsh.

Apatornis celer (MARSH)

Ichthyornis celer MARSH, Amer. Journ. Sci., ser. 3, vol. 5, 1873, p. 74.

Upper Cretaceous (Niobrara formation): Butte Creek, Logan County, near Smoky Hill River, Kansas.

Superorder NEOGNATHIAE: TYPICAL BIRDS

Order CAENAGNATHIFORMES: CAENAGNATHUS

Family CAENAGNATHIDAE: CAENAGNATHUS

Genus CAENAGNATHUS Sternberg

Caenagnathus STERNBERG, Journ. Pal., vol. 14, January 1940, p. 81. Type, by original designation, *Caenagnathus collinsi* Sternberg.

Caenagnathus collinsi STERNBERG⁴

Caenagnathus collinsi STERNBERG, Journ. Pal., vol. 14, January 1940, p. 81, figs. 1-6.

Upper Cretaceous (Pale beds, Belly River series): Quarry No. 112, Steveville map area, near mouth of Sand Creek, Alberta, Canada.

⁴ This interesting species, known from a nearly complete mandible, is listed in the above superorder tentatively. It is not absolutely certain that it is avian.

Order GAVIIFORMES: LOONS

Family GAVIIDAE: LOONS

Subfamily GAVIINAE

Genus GAVIA Forster

Gavia J. R. FORSTER, Enchirid. Hist. Nat., 1788, p. 38. Type, by subsequent designation, *Colymbus imber* Gunnerus = *C. immer* Brünnich (Allen, 1907).

***Gavia immer* (BRÜNNICH): Common Loon**

Colymbus Immer BRÜNNICH, Orn. Borealis, 1764, p. 38.

Modern form reported from late Pleistocene (Palos Verdes sand): Newport Bay, Orange County, California.

***Gavia arctica* (LINNAEUS): Arctic Loon**

Colymbus arcticus LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 135.

Modern form reported from late Pleistocene (Palos Verdes sand): San Pedro, Los Angeles County, California.

***Gavia concinna* WETMORE**

Gavia concinna WETMORE, Journ. Morph., vol. 66, No. 1, Jan. 2, 1940, p. 25, figs. 1-4.

Pliocene (Etchegoin formation): Sweetwater Canyon (type locality), 5½ miles east of King City, Monterey County, California. Middle Pliocene (San Diego formation): Washington Boulevard Freeway, San Diego, California. Pliocene (Bone Valley formation): near Brewster, Polk County, Florida.

***Gavia palaeodytes* WETMORE**

Gavia palaeodytes WETMORE, Proc. New England Zool. Club, vol. 22, June 23, 1943, p. 64, figs. 1-2.

Middle Pliocene (Bone Valley formation): Pierce (type locality) and Brewster, Polk County, Florida.

***Gavia howardae* BRODKORB**

Gavia howardae BRODKORB, Condor, vol. 55, No. 4, July 20, 1953, p. 212, fig. 1B.

Pliocene (Bone Valley formation): Pierce (type locality) and Brewster, Polk County, Florida.

Subfamily GAVIELLINAE: GAVIELLA

Genus GAVIELLA Wetmore

Gaviella WETMORE, Journ. Morph. vol. 66, Jan. 2, 1940, p. 28. Type, by original designation, *Gavia pusilla* Shufeldt.

Gaviella pusilla (SHUFELDT)

Gavia pusilla SHUFELDT, Trans. Connecticut Acad. Arts Sci., vol. 19, February 1915, p. 70, pl. 13, fig. 106.

Probably from Oligocene (White River formation): near Lusk, Wyoming.⁵

Order COLYMBIFORMES: GREBES

Family COLYMBIDAE: GREBES

Genus **COLYMBUS** Linnaeus

Colymbus LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 135. Type, by subsequent designation, *Colymbus cristatus* Linnaeus (Baird, Brewer, and Ridgway, 1884).

Subgenus **DYTES** Kaup

Dytes KAUP, Skizz. Entw.-Gesch. Eur. Thierw., 1829, p. 41. Type, by subsequent designation, *Dytes cornutus* Kaup = *Colymbus auritus* Linnaeus (Gray, 1842).

Colymbus auritus LINNAEUS: Horned Grebe

Colymbus auritus LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 135.

Modern form reported from Pleistocene: Cavern deposits of Tennessee; Seminole Field, Pinellas County, and Itchtucknee River, Columbia County, Florida.⁶

Colymbus caspicus HABLIZL: Eared Grebe

Colymbus caspicus HABLIZL, Neue Nordische Beyträge, vol. 4, 1783, p. 9.

Modern form reported from Pliocene (Ogallala formation): Edson Quarry, Sherman County, Kansas. Late Pleistocene: Fossil Lake, Oregon; San Pedro (Palos Verdes sand, lumberyard locality), Los Angeles County, California; Meade County (Vanhem formation, Jones fauna), Kansas.

Colymbus oligoceanus SHUFELDT

Colymbus oligoceanus SHUFELDT, Trans. Connecticut Acad. Arts Sci., vol. 19, February 1915, p. 54.

? Oligocene (John Day): Lower Willow Creek, Baker County, Oregon.

⁵ See Wetmore, A., Journ. Morph., vol. 66, Jan. 2, 1940, p. 30.

⁶ Specimens from Fossil Lake, Oregon, formerly included under this species have been found by Hildegard Howard to represent *Colymbus caspicus* and *Podilymbus podiceps*.

Colymbus parvus SHUFELDT

Colymbus parvus SHUFELDT, Bull. Amer. Mus. Nat. Hist., vol. 32, art. 6, July 9, 1913, p. 136, pl. 39, fig. 477.

Pliocene (Tulare formation): Kern County, California. Middle Pliocene (San Diego formation): San Diego, California. Late Pleistocene: Fossil Lake (type locality), Oregon.

Genus PLIODYTES Brodkorb

Pliodytes BRODKORB, Ann. Mag. Nat. Hist., ser. 12, vol. 6, December 1953, p. 953, 1 fig. Type, by original designation, *Pliodytes lanquisti* Brodkorb.

Pliodytes lanquisti BRODKORB

Pliodytes lanquisti BRODKORB, Ann. Mag. Nat. Hist., ser. 12, vol. 6, December 1953, p. 953, 1 fig.

Pliocene (Bone Valley formation): Near Brewster, Polk County, Florida.

Genus AECHMOPHORUS Coues

Aechmophorus COUES, Proc. Acad. Nat. Sci. Philadelphia, vol. 14, No. 5, April-May (Aug. 1), 1862, p. 229. Type, by original designation, *Podiceps occidentalis* Lawrence.

Aechmophorus occidentalis (LAWRENCE): Western Grebe

Podiceps occidentalis LAWRENCE, in Baird, Cassin, and Lawrence, Rep. Expl. and Surv. R. R. Pac., vol. 9, 1858, pp. liv, 892, 894.

Modern form reported from late Pleistocene: Rodeo, San Francisco Bay region.

Aechmophorus lucasi MILLER

Aechmophorus lucasi L. H. MILLER, Univ. California Publ., Bull. Dept. Geol., vol. 6, No. 4, Feb. 4, 1911, p. 83, figs. 1-3.

Late Pleistocene: Fossil Lake (type locality), Oregon;⁷ Palos Verdes sand, Newport Bay, Orange County, Playa del Rey, San Pedro, Los Angeles County, and near Manix, San Bernardino County, California.

⁷ Includes various specimens formerly listed under *Colymbus grisegena* and *Aechmophorus occidentalis*. Hildegard Howard (Carnegie Inst. Washington Publ. 551, Jan. 25, 1946, pp. 148-151) considers *lucasi* the Pleistocene ancestor of modern *A. occidentalis*, listing it as *Aechmophorus occidentalis lucasi*, the relationship being expressed in the sense of distribution through time rather than in the geographic sense of subspecies existing simultaneously.

Genus **PODILYMBUS** Lesson

Podilymbus LESSON, *Traité d'Orn.*, livr. 8, June 11, 1831, p. 595. Type, by monotypy, *Podiceps carolinensis* Latham = *Colymbus podiceps* Linnaeus,

Podilymbus podiceps (LINNAEUS): Pied-billed Grebe⁸

Colymbus Podiceps LINNAEUS, *Syst. Nat.*, ed. 10, vol. 1, 1758, p. 136.

Modern form reported from Pleistocene: Seminole Field, Pinellas County, Itchtucknee River, Columbia County, and Haile, Alachua County, Florida. Late Pleistocene: Fossil Lake, Oregon; Rancho La Brea, Los Angeles, and McKittrick, Kern County, California. Late Pleistocene or early Recent: Tepexpan, México.

Order PROCELLARIIFORMES: ALBATROSSES, SHEARWATERS,
PETRELS, and ALLIES

Family DIOMEDEIDAE: ALBATROSSES

Genus **DIOMEDEA** Linnaeus

Diomedea LINNAEUS, *Syst. Nat.*, ed. 10, vol. 1, 1758, p. 132. Type, by subsequent designation, *Diomedea exulans* Linnaeus (Gray, 1840).

Diomedea albatrus PALLAS: Short-tailed Albatross

Diomedea albatrus PALLAS, *Spic. Zool.*, vol. 1, fasc. 5, 1769, p. 28.

Modern form reported from late Pleistocene (Palos Verdes sand): Newport Bay, Orange County, Playa del Rey, Los Angeles County, California.

Diomedea anglica LYDEKKER

Diomedea anglica LYDEKKER, *Cat. Foss. Birds Brit. Mus.*, 1891, p. 189, fig. 42.

Pliocene (Bone Valley formation): Pierce, Polk County, Florida.⁹

Family PROCELLARIIDAE: SHEARWATERS and FULMARS

Genus **PUFFINUS** Brisson¹⁰

Puffinus BRISSON, *Orn.*, 1760, vol. 1, p. 56; vol. 6, p. 130. Type, by tautonymy, *Puffinus* Brisson = *Procellaria puffinus* Brünnich.

⁸ *Podilymbus magnus* Shufeldt, *Bull. Amer. Mus. Nat. Hist.*, vol. 32, art. 6, July 9, 1913, p. 136, pl. 38, figs. 439-440, 449, has been identified as *P. podiceps* by Wetmore, *California Acad. Sci.*, vol. 23, Dec. 30, 1937, pp. 198-199.

⁹ Described by Lydekker from the Upper Pliocene at Foxhall, Suffolk, England. Recorded from Florida by Wetmore, *Proc. New England Zool. Club*, vol. 22, June 23, 1943, pp. 66-67, pl. 12, figs. 10-15.

¹⁰ *Puffinus parvus* Shufeldt, *Ibis*, October 1916, p. 632, from Recent deposits in the bone caves of Bermuda is considered a synonym of *Puffinus lherminieri*. *Puffinus mcgalli* Shufeldt, *Ibis*, October 1916, p. 630, from Recent deposits in the bone caves of Bermuda seemingly is *Puffinus puffinus*.

Subgenus **PUFFINUS** Brisson**Puffinus griseus** (GMELIN): Sooty Shearwater

Procellaria grisea GMELIN, Syst. Nat., vol. 1, pt. 2, 1789, p. 564.

Modern form reported from late Pleistocene (Palos Verdes sand): Newport Bay, Orange County; near San Pedro (lumberyard locality) and Playa del Rey, Los Angeles County, California.

Puffinus puffinus (BRÜNNICH): Common Shearwater

Procellaria Puffinus BRÜNNICH, Orn. Borealis, 1764, p. 29.

Modern form reported from Pleistocene (Melbourne bone bed): Melbourne, Florida. Late Pleistocene (Palos Verdes sand): San Pedro and Playa del Rey, Los Angeles County, California.¹¹

Puffinus inceptor WETMORE

Puffinus inceptor WETMORE, Proc. California Acad. Sci., ser. 4, vol. 19, No. 8, July 15, 1930, p. 86, figs. 1-3.

Middle Miocene (Temblor formation): Sharktooth Hill, about 7 miles northeast of Bakersfield, California.

Puffinus diatomicus MILLER

Puffinus diatomicus L. H. MILLER, Carnegie Inst. Washington Publ. 349, August 1925, p. 111, pls. 1, 2, 7a.

Middle Miocene (Temblor formation, *Turritella ocoyana* zone): Lompoc (type locality). Miocene (Monterey shale): Lomita and San Pedro breakwater, San Pedro, California.

Puffinus kanakoffi HOWARD¹²

Puffinus kanakoffi HOWARD, Carnegie Inst. Washington Publ. 584, June 22, 1949, p. 187, pl. 2, figs. 3, 5.

Middle Pliocene (San Diego formation): Washington Boulevard Freeway, San Diego, California.

Puffinus felthami HOWARD¹²

Puffinus felthami HOWARD, Carnegie Inst. Washington Publ. 584, June 22, 1949, p. 194, pl. 2, figs. 4, 6.

Late Lower Pliocene: 3 miles north of Corona del Mar, Orange County, California.

¹¹ The California records refer to *Puffinus puffinus opisthomelas* Coues, formerly listed as a separate species.

¹² Subgeneric allocation provisional.

Subgenus ARDENNA Reichenbach

Ardenna REICHENBACH, Avium Syst. Nat., 1852 (1853), p. iv. Type, by monotypy, *Procellaria major* Faber = *P. gravis* O'Reilly.

***Puffinus conradi* MARSH**

Puffinus conradi MARSH, Amer. Journ. Sci., ser. 2, vol. 49, 1870, p. 212.

Middle Miocene (Calvert formation) : Maryland.

Genus FULMARUS Stephens

Fulmarus STEPHENS, in Shaw, Gen. Zoöl., vol. 13, pt. 1, Feb. 18, 1826, p. 233.

Type, by subsequent designation, *Procellaria glacialis* Linnaeus (Gray, 1855).

***Fulmarus glacialis* (LINNAEUS) : Fulmar**

Procellaria glacialis LINNAEUS, Fauna Suecica, ed. 2, 1761, p. 51.

Modern form reported from late Pleistocene (Palos Verdes sand) : Newport Bay, Orange County; San Pedro, Los Angeles County, California.

Family HYDROBATIDAE: STORM PETRELS**Genus OCEANODROMA Reichenbach**

Oceanodroma REICHENBACH, Avium Syst. Nat., 1852 (1853), p. iv. Type, by original designation, *Procellaria furcata* Gmelin.

***Oceanodroma hubbsi* MILLER**

Oceanodroma hubbsi L. H. MILLER, Condor, vol. 53, No. 2, Mar. 27, 1951, p. 78, fig. 1.

Upper Miocene (Capistrano formation¹³) : About 1 mile south of Capistrano Beach, Orange County, California.

Order PELECANIFORMES: TROPICBIRDS, PELICANS, FRIGATEBIRDS,
and ALLIES

Suborder PELECANI: PELICANS, BOOBIES, CORMORANTS, and DARTERS

Superfamily PELECANOIDEA: PELICANS and ALLIES

Family PELECANIDAE: PELICANS

Genus PELECANUS Linnaeus

Pelecanus LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 132. Type, by subsequent designation, *Pelecanus onocrotalus* Linnaeus (Gray, 1940).

¹³ Possibly Lower Pliocene.

Subgenus CYRTOPELICANUS Reichenbach

Cyrtopelicanus REICHENBACH, Avium Syst. Nat., 1852 (1853), p. vii. Type, by original designation, *Pelecanus trachyrhynchus* Latham = *P. erythrorhynchus* Gmelin.

***Pelecanus erythrorhynchus* Gmelin: White Pelican**

Pelecanus erythrorhynchus Gmelin, Syst. Nat., vol. 1, pt. 2, 1789, p. 571.

Modern form reported from late Pleistocene: Fossil Lake, Oregon; Manix lake beds, near Manix, San Bernardino County, California.
? Pleistocene: Rattlesnake Hill, Fallon, Nevada.

***Pelecanus halieus* Wetmore**

Pelecanus halieus WETMORE, Smithsonian Misc. Coll., vol. 87, No. 20, Dec. 27, 1933, p. 3, figs. 1-2.

Upper Pliocene (Hagerman lake beds): Near Hagerman, Idaho.

Subgenus LEPTOPELICANUS Reichenbach

Leptopelicanus REICHENBACH, Avium Syst. Nat., 1852 (1853), p. vii. Type, by original designation, *Pelecanus fuscus* Gmelin = *P. occidentalis* Linnaeus.

***Pelecanus occidentalis* Linnaeus: Brown Pelican**

Pelecanus occidentalis LINNAEUS, Syst. Nat., ed. 12, vol. 1, 1766, p. 215.

Modern form reported from late Pleistocene: Carpinteria, Santa Barbara County, California.

Family CYPHORNITHIDAE: CYPHORNITHES**Genus CYPHORNIS Cope**

Cyphornis COPE, Journ. Acad. Nat. Sci. Philadelphia, ser. 2, vol. 9, May 31, 1894, p. 449. Type, by monotypy, *Cyphornis magnus* Cope.

***Cyphornis magnus* Cope**

Cyphornis magnus COPE, Journ. Acad. Nat. Sci. Philadelphia, ser. 2, vol. 9, May 31, 1894, p. 451.

Middle Oligocene: Carmanah Point, Vancouver Island, British Columbia.

Genus PALAEOCHENŌIDES Shufeldt

Palaeochenoides SHUFELDT, Geol. Mag., n.s. 4, vol. 3, August 1916, p. 347. Type, by monotypy, *Palaeochenoides mioceanus* Shufeldt.

Palaeochenoides mioceanus SHUFELDT

Palaeochenoides mioceanus SHUFELDT, Geol. Mag., n.s. 4, vol. 3, August 1916, p. 347, pl. 15.

Miocene (Hawthorn formation): Near source of Stono River, South Carolina.

Superfamily SULOIDEA: BOOBIES, CORMORANTS, DARTERS, and ALLIES

Family SULIDAE: BOOBIES and GANNETS

Genus **SULA** Brisson

Sula BRISSON, Orn., 1760, vol. 1, p. 60; vol. 6, p. 494. Type, by tautonymy, *Sula* Brisson = *Pelecanus piscator* Linnaeus.

Subgenus **SULA** Brisson

***Sula stocktoni* MILLER**

Sula stocktoni L. H. MILLER, Publ. Univ. California at Los Angeles Biol. Sci., vol. 1, No. 5, Mar. 12, 1935, p. 75, fig. 2.

Middle Miocene (Monterey shale): Near Lomita, Los Angeles County, California.

***Sula willetti* MILLER**

Sula willetti L. H. MILLER, Carnegie Inst. Washington Publ. 349, August 1925, p. 112, pls. 3, 8, fig. 1.

Middle Miocene (Temblor formation, *Turritella ocoyana* zone): Lompoc, Santa Barbara County, California.

***Sula guano* BRODKORB**

Sula guano BRODKORB, Florida Geol. Surv. Rep. Invest. No. 14, November 1955, p. 9, figs. 2, 5, 8.

Pliocene (Bone Valley formation): Near Brewster, Polk County, Florida.

***Sula phosphata* BRODKORB**

Sula phosphata BRODKORB, Florida Geol. Surv. Rep. Invest. No. 14, November 1955, p. 11, figs. 3, 6, 9.

Pliocene (Bone Valley formation): Near Brewster, Polk County, Florida.

Subgenus **MICROSULA** Wetmore

Microsula WETMORE, Proc. U. S. Nat. Mus., vol. 85, Jan. 14, 1938, p. 25. Type, by original designation, *Sula* (*Microsula*) *avita* Wetmore.

***Sula avita* WETMORE**

Sula avita WETMORE, Proc. U. S. Nat. Mus., vol. 85, Jan. 14, 1938, p. 22, figs. 2-3.

Middle Miocene (Calvert formation): western shore of Chesapeake Bay, near Plumpoint, Calvert County, Maryland.

Genus MIOSULA Miller

Miosula L. H. MILLER, Carnegie Inst. Washington Publ. 349, August 1925, p. 114. Type, by monotypy, *Miosula media* Miller.

***Miosula media* MILLER**

Miosula media L. H. MILLER, Carnegie Inst. Washington Publ. 349, August 1925, p. 114, pl. 5.

Middle Miocene (Temblor formation, *Turritella ocoyana* zone): Lompoc, Santa Barbara County, California.

***Miosula recentior* HOWARD**

Miosula recentior HOWARD, Carnegie Inst. Washington Publ. 584, June 22, 1949, p. 190, pl. 2, figs. 1-2a.

Middle Pliocene (San Diego formation): Curlew Street, opposite Ostego Drive, San Diego, California.

Genus MORUS Vieillot

Morus VIEILLOT, Analyse, April 1816, p. 63. Type, by monotypy, *Pelecanus bassanus* Linnaeus.

***Morus loxostyla* (COPE)¹⁴**

Sula loxostyla COPE, Trans. Amer. Philos. Soc., n.s., vol. 14, December 1870, p. 236, fig. 53.

Miocene: Calvert County (type locality), Maryland; New Jersey.

***Morus vagabundus* WETMORE**

Morus vagabundus WETMORE, Proc. California Acad. Sci., ser. 4, vol. 19, No. 8, July 15, 1930, p. 89, fig. 4.

Middle Miocene (Temblor formation): Sharktooth Hill (type locality), about 7 miles northeast, and west branch of Granite Creek, 11 miles north of Bakersfield, California.

¹⁴ *Sula atlantica* Shufeldt, Trans. Connecticut Acad. Arts Sci., vol. 19, February 1915, p. 62, pl. 15, fig. 123, from the Miocene of New Jersey, is considered a synonym of *M. loxostyla*; cf. Wetmore, Auk, 1926, p. 465.

Morus lompocana (MILLER)

Sula lompocana L. H. MILLER, Carnegie Inst. Washington Publ. 349, August 1925, p. 114, pls. 4, 7b, 9.

Middle Miocene (Temblor formation, *Turritella ocoyana* zone): Lompoc, Santa Barbara County, California.

Morus peninsularis BRODKORB

Morus peninsularis BRODKORB, Florida Geol. Surv. Rep. Invest. No. 14, November 1955, p. 8, figs. 1, 4, 7.

Pliocene (Bone Valley formation): Near Brewster, Polk County, Florida.

Morus reykana HOWARD

Morus reykana HOWARD, Condor, vol. 38, No. 5, Sept. 15, 1936, p. 213, fig. 37.

Late Pleistocene (Palos Verdes sand): Newport Bay, Orange County; Playa del Rey (type locality), Los Angeles County, California.

Family PHALACROCORACIDAE: CORMORANTS

Genus GRACULAVUS Marsh¹⁵

Graculavus MARSII, Amer. Journ. Sci., ser. 3, vol. 3, 1872, p. 363. Type, by subsequent designation, *Graculavus velox* Marsh (Hay, 1902).

Graculavus pumilus MARSH

Graculavus pumilus MARSH, Amer. Journ. Sci., ser. 3, vol. 3, 1872, p. 364.

Paleocene (Hornerstown marl): Hornerstown, New Jersey.

Graculavus velox MARSII

Graculavus velox MARSII, Amer. Journ. Sci., ser. 3, vol. 3, 1872, p. 363.

Paleocene (Hornerstown marl): Hornerstown, New Jersey.

Genus PHALACROCORAX Brisson¹⁶

Phalacrocorax BRISSON, Orn., 1760, vol. 1, p. 60; vol. 6, p. 511. Type, by tautonymy, *Phalacrocorax* Brisson = *Pelecanus carbo* Linnaeus.

Phalacrocorax wetmorei BRODKORB

Phalacrocorax wetmorei BRODKORB, Florida Geol. Surv. Rep. Invest. No. 14, November 1955, p. 12, figs. 10, 11.

Pliocene (Bone Valley formation): Near Brewster, Polk County, Florida.

¹⁵ *Limosavis* Shufeldt, Trans. Connecticut Acad. Arts Sci., vol. 19, February 1915, p. 19, proposed as a new genus for *Graculavus velox* Marsh, is a synonym of *Graculavus* Marsh, as both names are based on the same species.

¹⁶ No subgenera are recognized in recent studies of the cormorants.

Phalacrocorax auritus (LESSON): Double-crested Cormorant

Carbo auritus LESSON, *Traité d'Orn.*, livr. 8, June 11, 1831, p. 605.

Modern form reported from Pliocene: Dry Creek, Malheur County, Oregon. Upper Pliocene (Hagerman lake beds): Near Hagerman, Idaho. Pleistocene: Melbourne (stratum 2), Sarasota, Bradenton, Seminole Field, Pinellas County, Itchtucknee River, and Vero, Florida. Late Pleistocene (Palos Verdes sand): Santa Monica and San Pedro, Los Angeles County, California. ? Pleistocene: Rattlesnake Hill, Fallon, Nevada.

Phalacrocorax penicillatus (BRANDT): Brandt's Cormorant

Carbo penicillatus BRANDT, *Bull. Sci. Acad. Imp. Sci. St.-Pétersbourg*, vol. 3, No. 4, Nov. 16, 1837, col. 55.

Modern form reported from late Pleistocene (Palos Verdes sand): Newport Bay, Orange County; Santa Monica and San Pedro (lumberyard locality), Los Angeles County, California.

Phalacrocorax femoralis MILLER

Phalacrocorax femoralis L. H. MILLER, *Condor*, vol. 31, No. 4, July 15, 1929, p. 167, figs. 58-59.

Upper Miocene (Modelo formation): Calabasas, Los Angeles County, California.

Phalacrocorax idahensis (MARSH)

Graculus idahensis MARSH, *Amer. Journ. Sci.*, ser. 2, vol. 49, 1870, p. 216.

Pliocene: Castle Creek; Owyhee County (type locality), Idaho; Pliocene (Bone Valley formation): Near Brewster, Polk County, Florida. Upper Pliocene (Hagerman lake beds): Near Hagerman, Idaho.

Phalacrocorax macropus (COPE)

Graculus macropus COPE, *Bull. Geol. Geogr. Surv. Terr.*, vol. 4, No. 2, 1878, p. 386.

Late Pleistocene: Fossil Lake, Oregon.¹⁷

Phalacrocorax marinavis SHUFELDT

Phalacrocorax marinavis SHUFELDT, *Trans. Connecticut Acad. Sci.*, vol. 19, February 1915, p. 56, pl. 14, figs. 114, 116-118, 122.

? Oligocene (John Day): Willow Creek, Oregon.

¹⁷ Shufeldt, *Auk*, 1915, pp. 485-488, has identified material from the Miocene of Montana as this species, but examination of the specimen reveals that this is in error.

Phalacrocorax mediterraneus SHUFELDT

Phalacrocorax mediterraneus SHUFELDT, Trans. Connecticut Acad. Arts Sci., vol. 19, February 1915, p. 58, pl. 15, fig. 138.

Lower Oligocene (Chadron formation): Gerry's Ranch, Weld County, Colorado.

Phalacrocorax rogersi HOWARD

Phalacrocorax rogersi HOWARD, Condor, vol. 34, No. 3, May 16, 1932, p. 118, fig. 19.

Early Pleistocene (Santa Barbara formation): Veronica Springs Stone Quarry, near Santa Barbara, California.

Phalacrocorax kennelli HOWARD

Phalacrocorax kennelli HOWARD, Carnegie Inst. Washington Publ. 584, June 22, 1949, p. 188, pl. 3, figs. 7-8a.

Middle Pliocene (San Diego formation): Washington Boulevard Freeway, San Diego, California.

Family ANHINGIDAE: SNAKEBIRDS

Genus ANHINGA Brisson

Anhinga BRISSON, Orn., 1760, vol. 1, p. 60; vol. 6, p. 476. Type, by tautonymy and monotypy, *Anhinga* Brisson = *Plotus anhinga* Linnaeus.

Anhinga anhinga (LINNAEUS): Anhinga

Plotus Anhinga LINNAEUS, Syst. Nat., ed. 12, vol. 1, 1766, p. 218.

Modern form reported from Pleistocene (Melbourne bone bed): Melbourne (stratum 2), Florida.

Order CICONIIFORMES: HERONS, STORKS, and ALLIES

Suborder ARDEAE: HERONS, BITTERNS, and ALLIES

Family ARDEIDAE: HERONS and BITTERNS

Subfamily ARDEINAE: HERONS and EGRETS

Genus ARDEA Linnaeus¹⁸

Ardea LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 141. Type, by subsequent designation, *Ardea cinerea* Linnaeus (Gray, 1840).

¹⁸ *Ardea sellardsi* Shufeldt, Journ. Geol., January-February (January) 1917, p. 19, described from Vero (stratum 3), Florida, proves to be based on the tibiotarsus of *Melcagris gallopavo*. See Wetmore, Smithsonian Misc. Coll., vol. 85, No. 2, Apr. 13, 1931, p. 32.

***Ardea herodias* LINNAEUS: Great Blue Heron**

Ardea Herodias LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 143.

Modern form reported from Pleistocene: Melbourne,¹⁹ Itchtucknee River, Bradenton and Seminole Field, Pinellas County, Florida. Late Pleistocene: Fossil Lake, Oregon; Rancho La Brea, Los Angeles, and McKittrick, Kern County, California.

***Ardea polkensis* BRODKORB**

Ardea polkensis BRODKORB, Florida Geol. Surv. Rep. Invest. No. 14, November 1955, p. 17, figs. 13, 14, 15.

Pliocene (Bone Valley formation): Near Brewster, Polk County, Florida.

Genus CASMERODIUS Gloger

Casmerodius GLOGER, Hand- und Hilfsbuch Naturg., 1842 (1841), p. 412.

Type, by subsequent designation, *Ardea egretta* Gmelin (Salvadori, 1882).

***Casmerodius albus* (LINNAEUS): Common Egret**

Ardea alba LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 144.

Modern form reported from Pleistocene: Melbourne, Seminole Field, Pinellas County, and Venice, Florida. Late Pleistocene: Rancho La Brea, Los Angeles, California; Baños de Ciego Montero, Santa Clara Province, Cuba.

Genus LEUCOPHOYX Sharpe

Leucophoyx SHARPE, Bull. Brit. Orn. Club, vol. 3, Apr. 30, 1894, p. xxxix.

Type, by original designation and monotypy, *Ardea candidissima* Gmelin = *Ardea thula* Molina.

***Leucophoyx thula* (MOLINA): Snowy Egret**

Ardea Thula MOLINA, Sagg. Stor. Nat. Chili, 1782, p. 235.

Modern form reported from Pleistocene: Bradenton, Florida.

Genus HYDRANASSA Baird

Hydranassa BAIRD, in Baird, Cassin, and Lawrence, Rep. Expl. Surv. R. R. Pac., vol. 9, 1858, p. 660. Type, by original designation, *Ardea ludoviciana* Wilson = *Egretta ruficollis* Gosse.

***Hydranassa tricolor* (MÜLLER): Tricolored Heron**

Ardea tricolor P. L. S. MÜLLER, Natursyst. Suppl., 1776, p. 111.

Modern form reported from Pleistocene: Seminole Field, Pinellas County, Florida.

¹⁹ The record from Vero (stratum 3) is now considered Recent. See Cooke, C. W., Florida Geol. Surv. Geol. Bull. 29, 1945, pp. 306-307.

Genus **FLORIDA** Baird

Florida BAIRD, in Baird, Cassin, and Lawrence, Rep. Expl. and Surv. R. R. Pac., vol. 9, 1858, pp. xxi, xlv, 659, 671. Type, by monotypy, *Ardea caerulea* Linnaeus.

Florida caerulea (LINNAEUS): Little Blue Heron

Ardea caerulea LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 143.

Modern form reported from Pleistocene: Seminole Field, Pinellas County, Florida.

Genus **BUTORIDES** Blyth

Butorides BLYTH, Cat. Birds Mus. Asiatic Soc., 1849 (1852), p. 281. Type, by monotypy, *Ardea javanica* Horsfield.

Butorides virescens (LINNAEUS): Green Heron

Ardea virescens LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 144.

Modern form reported from Pleistocene: Seminole Field, Pinellas County, Florida. Late Pleistocene: Rancho La Brea, Los Angeles, California.

Genus **NYCTICORAX** Forster

Nycticorax T. FORSTER, Syn. Cat. Brit. Birds, 1817, p. 59. Type, by tautonymy and monotypy, *Nycticorax infaustus* Forster = *Ardea nycticorax* Linnaeus.

Nycticorax nycticorax (LINNAEUS): Black-crowned Night Heron

Ardea Nycticorax LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 142.

Modern form reported from Pleistocene: San Josecito Cave, Aramberri, Nuevo León, México; Bradenton, and Itchtucknee River, Florida. Late Pleistocene: McKittrick, Kern County, and Rancho La Brea, Los Angeles, California.

Genus **NYCTANASSA** Stejneger

Nyctanassa STEJNEGER, Proc. U. S. Nat. Mus., vol. 10, Aug. 3, 1887, p. 295. Type, by original designation, *Ardea violacea* Linnaeus.

Nyctanassa violacea (LINNAEUS): Yellow-crowned Night Heron

Ardea violacea LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 143.

Modern form reported from Pleistocene: Seminole Field, Pinellas County, Florida.²⁰

²⁰ *Larus vero* Shufeldt, Journ. Geol., 1917, p. 18, from stratum 3 of Vero, Florida, is *Nyctanassa violacea*, according to Wetmore, Smithsonian Misc. Coll., vol. 85, No. 2, 1931, pp. 3, 11, and 16. Cooke, Florida Geol. Surv., Geol. Bull. 29, 1945, pp. 306-307, considers this deposit to be of Recent age.

Genus EOCEORNIS Shufeldt

Eoecornis SHUFELDT, Trans. Connecticut Acad. Arts Sci., vol. 19, February 1915, p. 39. Type, by monotypy, *Eoecornis ardetta* Shufeldt.

***Eoecornis ardetta* SHUFELDT**

Eoecornis ardetta SHUFELDT, Trans. Connecticut Acad. Arts Sci., vol. 19, February 1915, p. 39, pl. 13, fig. 102.

Eocene (Bridger formation): Henry's Fork, Wyoming.

Subfamily BOTAURINAE: BITTERNS**Genus IXOBRYCHUS Billberg**

Ixobrychus BILLBERG, Syn. Faunae Scand., vol. 1, pt. 2, 1828, p. 166. Type, by subsequent designation, *Ardea minuta* Linnaeus (Stone, 1907).

***Ixobrychus exilis* (GMELIN): Least Bittern.**

Ardea exilis GMELIN, Syst. Nat., vol. 1, pt. 2, 1789, p. 645.

Modern form reported from late Pleistocene: Baños de Ciego Montero, Santa Clara Province, Cuba.

Genus BOTAURUS Stephens

Botaurus STEPHENS, in Shaw, Gen. Zoöl., vol. 11, pt. 2, August 1819, p. 592. Type, by subsequent designation, *Ardea stellaris* Linnaeus (Gray, 1840).

***Botaurus lentiginosus* (RACKETT): American Bittern**

Ardea lentiginosa RACKETT, in Pulteney, Cat. Birds, Shells and . . . Plants of Dorsetshire, ed. 2, May 1813, p. 14.

Modern form reported from Pleistocene: Seminole Field, Pinellas County, and Sarasota, Florida. Late Pleistocene: Fossil Lake, Oregon;²¹ Rancho La Brea, Los Angeles, California.

Genus BOTAUROIDES Shufeldt

Botauroides SHUFELDT, Trans. Connecticut Acad. Arts Sci., vol. 19, February 1915, p. 33. Type, by monotypy, *Botauroides parvus* Shufeldt.

***Botauroides parvus* SHUFELDT**

Botauroides parvus SHUFELDT, Trans. Connecticut Acad. Arts Sci., vol. 19, February 1915, p. 33.

Eocene (? Bridger formation): "Spanish John Meadow," Wyoming.

²¹ *Ardea paloccidentalis* Shufeldt described from Fossil Lake is based on a fragmentary tarsometatarsus of the American bittern. See Howard, Carnegie Inst. Washington Publ. 551, Jan. 25, 1946, pp. 156-157.

Suborder CICONIAE: STORKS, IBISES, and SPOONBILLS

Superfamily CICONIOIDEA: STORKS and WOOD IBISES

Family CICONIIDAE: STORKS and JABIRUS

Subfamily CICONIINAE: STORKS

Genus CICONIA Brisson

Ciconia BRISSON, Orn., 1760, vol. 1, p. 48; vol. 5, p. 361. Type, by tautonymy,
Ciconia = *Ardea ciconia* Linnaeus.

Ciconia maltha MILLER

Ciconia maltha L. H. MILLER, Univ. California Publ., Bull. Dept. Geol., vol. 5,
No. 30, Aug. 5, 1910, p. 440, figs. 1-7.

Upper Pliocene (Hagerman lake beds): Barbour Ranch, Snake River, Idaho. Pleistocene: American Falls, Idaho; Vero (stratum 2), Melbourne (stratum 2), Itchtucknee River, 6½ miles south of Marineland, Flagler County, Seminole Field, Pinellas County, and Venice, Florida. Late Pleistocene: Carpinteria, McKittrick, Rancho La Brea, Los Angeles (type locality), and near Manix, San Bernardino County, California; Baños de Ciego Montero, Santa Clara Province, Cuba.²²

Subfamily MYCTERIINAE: WOOD IBISES

Genus MYCTERIA Linnaeus

Mycteria LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 140. Type, by monotypy,
Mycteria americana Linnaeus.

Mycteria wetmorei HOWARD²³

Mycteria wetmorei HOWARD, Condor, vol. 37, Sept. 15, 1935, p. 253, fig. 47.
Late Pleistocene: Rancho La Brea, Los Angeles, California.

Superfamily THRESKIORNITHOIDEA: IBISES

Family THRESKIORNITHIDAE: IBISES and SPOONBILLS

Subfamily THRESKIORNITHINAE: IBISES

Genus PLEGADIS Kaup

Plegadis KAUP, Skizz. Entw.-Ges. Eur. Thierw., 1829, p. 82. Type, by monotypy, *Tantalus falcinellus* Linnaeus.

²² Records formerly listed as *Jabiru mycteria* (Lichtenstein) have all been assigned to the present species by Hildegard Howard, in Carnegie Inst. Washington Publ. 530, Jan. 19, 1942, p. 202. *Jabiru weillsi* Sellards, therefore, becomes a synonym of *Ciconia maltha*.

²³ Replaces *Mycteria americana* as listed in Check-list of North American Birds, ed. 4, 1931, p. 416.

Plegadis chihi (VIEILLOT): White-faced Ibis

Numenius chihi VIEILLOT, Nouv. Dict. Hist. Nat., nouv. éd., vol. 8, March 1817, p. 303.

Modern form reported from late Pleistocene: Rancho La Brea, Los Angeles, California.

Genus EUDOCIMUS Wagler

Eudocimus WAGLER, Isis von Oken, 1832, col. 1232. Type, by subsequent designation, *Scolopax rubra* Linnaeus (Reichenow, 1877).

Eudocimus albus (LINNAEUS): White Ibis

Scolopax alba LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 145.

Modern form reported from Pleistocene: Seminole Field, Pinellas County, and Haile, Alachua County, Florida.

Subfamily PLATALEINAE: SPOONBILLS**Genus AJAIA Reichenbach**

Ajaia REICHENBACH, Avium Syst. Nat., 1852 (1853), p. xvi. Type, by original designation, *Ajaia rosea* Reichenbach = *Platalca ajaja* Linnaeus.

Ajaia ajaja (LINNAEUS): Roseate Spoonbill

Platalca Ajaja LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 140.

Modern form reported from late Pleistocene: Rancho La Brea, Los Angeles, California.

Suborder PHOENICOPTERI: FLAMINGOS**Family PHOENICOPTERIDAE: FLAMINGOS****Genus PHOENICOPTERUS Linnaeus**

Phoenicopterus LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 139. Type, by monotypy, *Phoenicopterus ruber* Linnaeus.

Phoenicopterus copei SHUFELDT

Phoenicopterus copei SHUFELDT, Amer. Nat., vol. 25, No. 297, September 1891, p. 820.

Late Pleistocene: Fossil Lake, Oregon.

Phoenicopterus minutus HOWARD

Phoenicopterus minutus HOWARD, Geol. Surv. Prof. Pap. 264-J, June 1955, p. 202, pl. 50.

Late Pleistocene; Manix lake beds, near Manix, San Bernardino County, California.

Phoenicopterus stocki MILLER

Phoenicopterus stocki L. H. MILLER, Wilson Bull., vol. 56, No. 2, June 1944, p. 77, figs. 1, 2.

Pliocene (Rincón) : Chihuahua, México.

Phoenicopterus floridanus BRODKORB

Phoenicopterus floridanus BRODKORB, Chicago Acad. Sci. Nat. Hist. Misc., No. 124, June 9, 1953, p. 1, figs. 1-2.

Pliocene (Bone Valley formation) : Near Brewster, Polk County, Florida.

Family PALOELODIDAE: PALOELODUS and ALLIES

Genus MEGAPALOELODUS Miller

Megapaloclodus A. H. MILLER, Univ. California Publ., Bull. Dept. Geol. Sci., vol. 27, No. 4, June 22, 1944, p. 86. Type, by original designation, *Megapaloclodus connectens* A. H. Miller.

Megapaloelodus connectens MILLER

Megapaloelodus connectens A. H. MILLER, Univ. California Publ., Bull. Dept. Geol. Sci., vol. 27, No. 4, June 22, 1944, p. 86, fig. 1.

Lower Miocene (Rosebud formation) : Flint Hill, 9 miles west-southwest of Martin, Bennett County, South Dakota (type locality).
Upper Miocene (Barstow formation) : near Barstow, California.

Order ANSERIFORMES: SCREAMERS, DUCKS, GEESE, and SWANS

Suborder ANSERES: DUCKS, GEESE, SWANS, and ALLIES

Family PARANYROCIDAE: PARANYROCA

Genus PARANYROCA Miller and Compton

Paranyroca A. H. MILLER and L. V. COMPTON, Condor, vol. 41, No. 4, July 15, 1939, p. 153. Type, by original designation, *Paranyroca magna* Miller and Compton.

Paranyroca magna MILLER and COMPTON

Paranyroca magna A. H. MILLER and L. V. COMPTON, Condor, vol. 41, No. 4, July 15, 1939, p. 153, fig. 34 A, C, D, E.

Lower Miocene (Rosebud formation) : Flint Hill, 9 miles west-southwest of Martin, Bennett County, South Dakota.

Family ANATIDAE: DUCKS, GEESE, and SWANS

Subfamily CYGNINAE: SWANS

Genus CYGNUS Bechstein

Cygnus BECHSTEIN, Orn. Taschenb. Deutschl., vol. 2, 1803, p. 404, footnote. Type, by tautonymy, *Anas cygnus* Linnaeus.

Subgenus STHENELIDES Stejneger

Sthenelides STEJNEGER, Stand. Nat. Hist., vol. 4, 1885, p. 143. Type, by monotypy, *Anas melancoripha* Molina.

***Cygnus paloregonus* (COPE)²⁴**

Cygnus paloregonus COPE, Bull. Geol. Geogr. Surv. Terr., vol. 4, No. 2, 1878, p. 388.

Pleistocene: Froman's Ferry, Idaho. Late Pleistocene: Fossil Lake, Oregon (type locality).²⁵

Genus OLOR Wagler

Olor WAGLER, Isis von Oken, 1832, col. 1234. Type, by subsequent designation, *Cygnus musicus* Bechstein = *Anas cygnus* Linnaeus (Gray, 1840).

Subgenus OLOR Wagler***Olor columbianus* (ORD): Whistling Swan**

Anas columbianus ORD, in Guthrie, Geogr., 2d Amer. ed., 1815, p. 319.

Modern form reported from Pleistocene: Seminole Field, Pinellas County, Florida. Late Pleistocene: Rancho La Brea, Los Angeles, and McKittrick, Kern County, California.

Subgenus CLANGOCYCNUS Oberholser

Clangocycnus OBERHOLSER, Emu, vol. 8, pt. 1, July 1908, p. 3. Type, by monotypy, *Cygnus buccinator* Richardson.

***Olor buccinator* (RICHARDSON): Trumpeter Swan**

Cygnus buccinator RICHARDSON, in Wilson and Bonaparte, Amer. Orn., Jame-son ed., vol. 4, August 1831, p. 345.

Modern form reported from Pleistocene: Aurora, Illinois; Itchtucknee River, Florida. Late Pleistocene: Fossil Lake, Oregon.

Subfamily ANSERINAE: GEESE**Genus BRANTA Scopoli**

Branta SCOPOLI, Annus I, Historico-Naturalis, 1769, p. 67. Type, by subsequent designation, *Anas bernicla* Linnaeus (Bannister, 1870).

²⁴ Subgeneric allocation tentative.

²⁵ Specimens named *Cygnus matthewi* and *Anser condoni* by Shufeldt are now identified as *C. paloregonus*. See Howard, Carnegie Inst. Washington Publ. 551, Jan. 25, 1946, pp. 160, 162, 163.

***Branta canadensis* (LINNAEUS): Canada Goose**

Anas canadensis LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 123.

Modern form reported from Pleistocene: Santa Rosa Island, California; Seminole Field, Pinellas County, and Itchtucknee River, Florida. Early Pleistocene: Irvington, Alameda County, California. Late Pleistocene: Fossil Lake, Oregon; ²⁶ Potter Creek Cave, Shasta County; Rancho La Brea, Los Angeles, San Pedro, Los Angeles County, and near Manix, San Bernardino County, California. ? Pleistocene: Rattlesnake Hill, Fallon, Nevada.²⁷

***Branta canadensis hutchinsii* (RICHARDSON): Richardson's Goose**

Anser Hutchinsii RICHARDSON, in Swainson and Richardson, Fauna Bor.-Amer., vol. 2, 1831 (1832), p. 470.

Modern form reported from Pleistocene: Seminole Field, Pinellas County, Itchtucknee River, and Melbourne, Florida.

***Branta bernicla* (LINNAEUS): Brant**

Anas bernicla LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 124.

Modern form reported from Pleistocene: Fossil Lake, Oregon.

***Branta esmeralda* BURT**

Branta esmeralda BURT, Univ. California Publ., Bull. Dept. Geol. Sci., vol. 18, No. 6, Mar. 19, 1929, p. 222, pl. 20.

Upper Miocene (Esmeralda formation): Fish Lake Valley, Esmeralda County, Nevada.

***Branta howardae* MILLER**

Branta howardae L. H. MILLER, Condor, vol. 32, No. 4, July 15, 1930, p. 208, fig. 74.

Lower Pliocene (Ricardo formation): Mojave Desert area, Kern County, California.

***Branta dickeyi* MILLER**

Branta dickeyi L. H. MILLER, Condor, vol. 26, No. 5, Sept. 15, 1924, p. 179, fig. 46.

Upper Pliocene: Dry Creek, Malheur County, Oregon. Late Pleistocene: McKittrick, California.

²⁶ Specimens from Fossil Lake range in size from modern *B. c. minima* to *B. c. canadensis*.

²⁷ Recorded as *Branta canadensis canadensis*.

Branta hysibata (COPE)²⁸

Anser hysibatus COPE, Bull. Geol. Geogr. Surv. Terr., vol. 4, No. 2, 1878, p. 387.

Late Pleistocene: Fossil Lake, Oregon.

Branta propinqua SHUFELDT

Branta propinqua SHUFELDT, Journ. Acad. Nat. Sci. Philadelphia, 2d ser., vol. 9, sign. 53, Oct. 20, 1892, p. 407, pl. 15, fig. 17.

Late Pleistocene: Fossil Lake, Oregon.

Genus ANABERNICULA Ross²⁹

Anabernicula Ross, Trans. San Diego Soc. Nat. Hist., vol. 8, No. 15, Aug. 24, 1935, p. 107. Type, by monotypy, *Anabernicula gracilentia* Ross = *Branta minuscula* Wetmore.³⁰

Anabernicula minuscula (WETMORE)

Branta minuscula WETMORE, Proc. U. S. Nat. Mus., vol. 64, art. 5, Jan. 15, 1924, p. 6, figs. 3-4.

Upper Pliocene (Blancan): Near Benson, Arizona (type locality).
Late Pleistocene: Fossil Lake, Oregon; McKittrick, Kern County, and Rancho La Brea, Los Angeles, California. Quaternary: Smith Creek Cave, 34 miles north of Baker, White Pine County, Nevada.

Genus PRESBYCHEN Wetmore

Presbychen WETMORE, Proc. California Acad. Sci., ser. 4, vol. 19, No. 8, July 15, 1930, p. 92. Type, by original designation, *Presbychen abavus* Wetmore.

Presbychen abavus WETMORE

Presbychen abavus WETMORE, Proc. California Acad. Sci., ser. 4, vol. 19, No. 8, July 15, 1930, p. 92, figs. 5-7.

Miocene (Temblor formation): Sharktooth Hill, Kern County, about 7 miles northeast of Bakersfield, California.

Genus ANSER Brisson

Anser BRISSON, Orn., 1760, vol. 1, p. 58; vol. 6, p. 261. Type, by tautonymy, *Anser domestica* Brisson = *Anas anser* Linnaeus.

²⁸ Status doubtful. Howard, Carnegie Inst. Washington Publ. 551, Jan. 25, 1946, pp. 167-169, indicates that this may be a synonym of *Chen hyperborea*.

²⁹ Possibly representative of a distinct subfamily. See Howard, Carnegie Inst. Washington Publ. 551, Jan. 25, 1946, pp. 172-173.

³⁰ See Howard, Condor, 1936, p. 35.

Anser albifrons (SCOPOLI) : White-fronted Goose

Branta albifrons SCOPOLI, Annus I, Historico-Naturalis, 1769, p. 69.

Modern form reported from late Pleistocene : Fossil Lake, Oregon ; Rancho La Brea, Los Angeles, and San Pedro ³¹ (Palos Verdes sand), Los Angeles County, California.

Genus CHEN Boie

Chen BOIE, Isis von Oken, vol. 10, Heft 5, 1822, col. 563. Type, by monotypy, *Anser hyperboreus* Pallas.

Chen hyperborea (PALLAS) : Snow Goose

Anser hyperboreus PALLAS, Spic. Zool., vol. 1, fasc. 6, 1769, p. 25.

Modern form reported from late Pleistocene : Fossil Lake, Oregon ; Rancho La Brea, Los Angeles, and McKittrick, California.³²

Chen rossii (CASSIN) : Ross' Goose

Anser Rossii "Baird," CASSIN, Proc. Acad. Nat. Sci. Philadelphia, vol. 13, sign. 5-6, March-April (June 30), 1861, p. 73.

Modern form reported from late Pleistocene : Fossil Lake, Oregon.

Chen pressa WETMORE ³³

Chen pressa WETMORE, Smithsonian Misc. Coll., vol. 87, No. 20, Dec. 27, 1933, p. 9, figs. 5-8.

Upper Pliocene (Hagerman lake beds) : Near Hagerman, Idaho.

Subfamily DENDROCYGNINAE : TREEDUCKS**Genus DENDROCYGNA Swainson**

Dendrocygna SWAINSON, Class. Birds, vol. 2, July 1, 1837, p. 365. Type, by subsequent designation, *Anas arcuata* Horsfield (Gray, 1840).

Dendrocygna eversa WETMORE

Dendrocygna eversa WETMORE, Proc. U. S. Nat. Mus., vol. 64, art. 5, Jan. 15, 1924, p. 3, figs. 1-2.

Upper Pliocene (Blancan) : Near Benson, Arizona.

³¹ Specimen with size of the subspecies *frontalis*.

³² *Chen caerulescens* recorded by Shufeldt, Bull. Amer. Mus. Nat. Hist., vol. 32, July 9, 1913, p. 145, on basis of scapula only, has been dropped. See Howard, Carnegie Inst. Washington Publ. 551, Jan. 25, 1946, p. 166?

³³ Miller, A. H., Univ. California Publ. Zool., vol. 42, No. 1, 1937, p. 41, suggests that this species may belong in the genus *Nesochen*.

Genus DENDROCHEN Miller

Dendrochen A. H. MILLER, Univ. California Publ., Bull. Dept. Geol. Sci., vol. 27, No. 4, June 22, 1944, p. 88. Type, by original designation, *Dendrochen robusta* Miller.

***Dendrochen robusta* MILLER**

Dendrochen robusta A. H. MILLER, Univ. California Publ., Bull. Dept. Geol. Sci., vol. 27, No. 4, June 22, 1944, p. 88, fig. 3.

Lower Miocene (Rosebud formation): Flint Hill, 9 miles west-southwest of Martin, Bennett County, South Dakota.

Subfamily ANATINAE: SURFACE-FEEDING DUCKS**Genus ANAS Linnaeus**

Anas LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 122. Type, by subsequent designation, *Anas boschas* Linnaeus = *A. platyrhynchos* Linnaeus (Lesson, 1828).

***Anas platyrhynchos* LINNAEUS: Mallard**

Anas platyrhynchos LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 125.

Modern form reported from late Pleistocene: Fossil Lake, Oregon; Rancho La Brea, Los Angeles, McKittrick, and Carpinteria, California; (Palos Verdes sand): San Pedro, Los Angeles County, California; Baños de Ciego Montero, Santa Clara Province, Cuba. Pleistocene: Itchtucknee River, and Haile, Alachua County, Florida.

***Anas rubripes* BREWSTER: Black Duck**

Anas obscura rubripes BREWSTER, Auk, vol. 19, No. 2, April 1902, p. 184.

Modern form reported from Pleistocene: Itchtucknee River, Florida.

***Anas fulvigula* RIDGWAY: Mottled Duck**

Anas obscura var. *fulvigula* RIDGWAY, Amer. Nat., vol. 8, No. 2, February 1874, p. 111.

Modern form reported from Pleistocene: Seminole Field, Pinellas County, Itchtucknee River, and Bradenton, Florida.

***Anas strepera* LINNAEUS: Gadwall**

Anas strepera LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 125.

Modern form reported from late Pleistocene: McKittrick and Rancho La Brea, Los Angeles, California.³⁴

³⁴ Listed erroneously in Check-list of North American Birds, ed. 4, 1931, p. 421, from Itchtucknee River, Florida.

Anas acuta LINNAEUS: Pintail

Anas acuta LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 126.

Modern form reported from late Pleistocene: Fossil Lake, Oregon. (Vanhem formation, Jones fauna): Meade County, Kansas.

Anas carolinensis GMELIN; Green-winged Teal³⁵

Anas carolinensis GMELIN, Syst. Nat., vol. 1, pt. 2, 1789, p. 533.

Modern form reported from Pleistocene: Santa Rosa Island, California; Seminole Field, Pinellas County, Florida. Late Pleistocene: Fossil Lake, Oregon; Hawver Cave, Eldorado County, McKittrick, Kern County, Rancho La Brea, Los Angeles, and San Pedro, Los Angeles County, California; McPherson County, Kansas (Kentuck locality).

Anas bunkeri (WETMORE)

*Nettion bunker*i WETMORE, Univ. Kansas Sci. Bull., vol. 30, pt. 1, No. 9, May 15, 1944, p. 92, figs. 1-3.

Upper Pliocene (Rexroad formation): Meade County, Kansas (type locality); 2 miles south of Benson, Arizona.

Anas cyanoptera VIEILLLOT: Cinnamon Teal

Anas cyanoptera VIEILLLOT, Nouv. Dict. Hist. Nat., nouv. éd., vol. 5, December 1816, p. 104.

Modern form reported from late Pleistocene: Fossil Lake, Oregon; McKittrick, Kern County, California.

Anas integra (MILLER).

Querquedula integra A. H. MILLER, Univ. California Publ., Bull. Dept. Geol. Sci., vol. 27, No. 4, June 22, 1944, p. 90, fig. 4.

Lower Miocene (Rosebud formation), Flint Hill, 9 miles west-southwest of Martin, Bennett County, South Dakota.

Genus MARECA Stephens

Mareca STEPHENS, in Shaw, Gen. Zool., vol. 12, pt. 2, 1824, p. 130. Type, by subsequent designation, *Mareca fistularis* Stephens = *Anas penelope* Linnaeus (Eyton, 1838).

³⁵ There are also records for the Upper Miocene or lower Pliocene of Cedar Mountain, Nevada, by L. H. Miller, Univ. California Publ., Bull. Dept. Geol., vol. 9, Feb. 23, 1916, p. 173, and from the lower Pliocene of Hemphill County, Texas, by Compton, Condor, vol. 36, No. 1, January 1934, pp. 40-41, based on fragmentary material that is open to question as to specific identity.

Mareca americana (GMELIN): American Widgeon

Anas americana GMELIN, Syst. Nat., vol. 1, pt. 2, 1789, p. 526.

Modern form reported from late Pleistocene: Fossil Lake, Oregon; McKittrick, Kern County; San Pedro (Palos Verdes sand, lumberyard locality), Los Angeles County, California.

Genus SPATULA Boie

Spatula BOIE, Isis von Oken, vol. 10, Heft 5, 1822, col. 564. Type, by monotypy, *Anas clypeata* Linnaeus.

Spatula clypeata (LINNAEUS): Shoveler

Anas clypeata LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 124.

Modern form reported from late Pleistocene: Fossil Lake, Oregon;³⁶ McKittrick, Kern County, and San Pedro (Palos Verdes sand, lumberyard locality), Los Angeles County, California; Meade County (Vanhem formation, Jones fauna), Kansas.

Subfamily AYTHYINAE: DIVING DUCKS³⁷**Genus AYTHYA Boie**

Aythya BOIE, Tageb. Reise Norwegen, before May 1822, p. 351. Type, by monotypy, *Anas marila* Linnaeus.

Aythya americana (EYTON): Redhead

Fuligula americana EYTON, Mon. Anatidae, 1838, p. 155.

Modern form reported from late Pleistocene: Fossil Lake, Oregon; McKittrick, California.

Aythya collaris (DONOVAN): Ring-necked Duck

Anas collaris DONOVAN, Brit. Birds, vol. 6, 1809, pl. 147.

Modern form reported from Lower Pliocene: Cedar Mountain, Nevada.

³⁶ Shufeldt's record of *Aix sponsa* from Fossil Lake is now assigned to *Spatula clypeata*. See Howard, Carnegie Inst. Washington Publ. 551, Jan. 25, 1946, p. 176.

³⁷ *Polysticta stelleri*, *Bucephala islandica*, and *Histrionicus histrionicus* reported from Fossil Lake by Shufeldt were wrongly identified and are eliminated from the list. See Howard, Carnegie Inst. Washington Publ. 551, Jan. 25, 1946, p. 176.

Aythya valisineria (WILSON): Canvasback

Anas valisineria WILSON, Amer. Orn., vol. 8, 1814, p. 103, pl. 70, fig. 5.

Modern form reported from Pleistocene: Itchtucknee River, Florida.³⁸

Aythya affinis (EYTON): Lesser Scaup

Fuligula affinis EYTON, Mon. Anatidae, 1838, p. 157.

Modern form reported from Pleistocene: Melbourne (stratum 2), Itchtucknee River, Seminole Field, Pinellas County, Venice, and cave deposits near Lecanto, Florida. Late Pleistocene: Fossil Lake, Oregon.

Genus BUCEPHALA Baird

Bucephala BAIRD, in Baird, Cassin, and Lawrence, Rep. Expl. Surv. R. R. Pac., vol. 9, 1858, pp. XXIII, L, 787, 788, 795. Type, by original designation, *Anas albeola* Linnaeus.

Bucephala albeola (LINNAEUS): Bufflehead

Anas Albeola LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 124.

Modern form reported from Upper Pliocene (Rexroad formation): Meade County, Kansas. Pleistocene: Seminole Field, Pinellas County, Florida. Late Pleistocene: Fossil Lake, Oregon; McKittrick, Kern County, and San Pedro (Palos Verdes sand, lumberyard locality), Los Angeles County, California.

Bucephala ossivallis BRODKORB

Bucephala ossivallis BRODKORB, Florida Geol. Surv. Rep. Invest. No. 14, November 1955, p. 18, figs. 16, 17.

Pliocene (Bone Valley formation): Near Brewster, Polk County, Florida.

Genus CLANGULA Leach

Clangula LEACH, in Ross, Voy. Discovery, 1819, app., p. XLVIII. Type, by monotypy, *Clangula glacialis* Linnaeus = *Anas hyemalis* Linnaeus.

Clangula hyemalis (LINNAEUS): Oldsquaw

Anas hyemalis LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 126.

Modern form reported from late Pleistocene: Fossil Lake, Oregon.

Genus MELANITTA Boie

Melanitta BOIE, Isis von Oken, vol. 10, Heft 5, 1822, col. 564. Type, by subsequent designation, *Anas fusca* Linnaeus (Eyton, 1838).

³⁸ Shufeldt's record for Fossil Lake, Oregon, refers to *Anas acuta*. See Howard, Carnegie Inst. Washington Publ. 551, Jan. 25, 1946, p. 174.

Melanitta deglandi (BONAPARTE): White-winged Scoter

Oedemia deglandi BONAPARTE, Rev. Crit. Orn. Europe, 1850, p. 108.

Modern form reported from late Pleistocene (Palos Verdes sand): San Pedro, Los Angeles County, California.

Melanitta perspicillata (LINNAEUS): Surf Scoter

Anas perspicillata LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 125.

Modern form reported from late Pleistocene: Fossil Lake, Oregon; San Pedro (Palos Verdes sand), Los Angeles County, California.

Genus CHENDYTES Miller

Chendytes L. H. MILLER, Condor, vol. 27, No. 4, July 15, 1925, p. 145. Type, by monotypy, *Chendytes lawi* Miller.

Chendytes lawi MILLER

Chendytes lawi L. H. MILLER, Condor, vol. 27, No. 4, July 15, 1925, p. 145, fig. 40.

Early Pleistocene: Sexton Canyon, near Lake Canyon, Ventura County. Late Pleistocene: Newport Bay, Orange County; Lomita, Playa del Rey, Santa Monica (type locality), San Pedro (lumberyard locality), Vermont and Sepulveda Boulevard, Bixby Slough near Hermosa Beach, and Palos Verdes, Los Angeles County, California.

Chendytes milleri HOWARD

Chendytes milleri H. HOWARD, Condor, vol. 57, No. 3, May 25, 1955, p. 137, fig. 1 a, d, e, f, g, i, fig. 2 b, c, fig. 3.

Early Pleistocene: San Nicolás Island, California.

Subfamily OXYURINAE: RUDDY and MASKED DUCKS**Genus OXYURA Bonaparte**

Oxyura BONAPARTE, Ann. Lyc. Nat. Hist. New York, vol. 2, 1828, p. 390. Type, by monotypy, *Anas rubidus* Wilson.

Oxyura jamaicensis (GMELIN): Ruddy Duck

Anas jamaicensis GMELIN, Syst. Nat., vol. 1, pt. 2, 1789, p. 519.

Modern form reported from Pleistocene: Venice, Florida. Late Pleistocene: Fossil Lake, Oregon; McKittrick, Kern County, and near Manix, San Bernardino County, California.

Subfamily EONESSINAE: EONESSA**Genus EONESSA Wetmore**

Eonessa WETMORE, Journ. Pal., vol. 12, No. 3, May 1938, p. 280. Type, by original designation, *Eonessa anaticula* Wetmore.

Eonessa anaticula WETMORE

Eonessa anaticula WETMORE, Journ. Pal., vol. 12, No. 3, May 1938, p. 280, figs. 1-5.

Eocene (Uinta C horizon): Myton Pocket, Utah.

Subfamily MERGINAE: MERGANSERS

Genus **LOPHODYTES** Reichenbach

Lophodytes REICHENBACH, Avium Syst. Nat., 1852 (1853), p. ix. Type, by original designation, *Mergus cucullatus* Linnaeus.

Lophodytes cucullatus (LINNAEUS): Hooded Merganser³⁹

Mergus cucullatus LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 120.

Modern form reported from Pleistocene: Seminole Field, Pinellas County, Venice, and Itchtucknee River, Florida; Nye Sink, Beaver County, Oklahoma. Late Pleistocene: McPherson County (Kentuck locality), Kansas.

Lophodytes floridana (SHUFELDT)⁴⁰

Querquedula floridana SHUFELDT, 9th Ann. Rep. Florida State Geol. Surv., 1917, p. 36, pl. 1, fig. 4, pl. 2, fig. 25.

Pleistocene: Vero (stratum 2, type locality), Melbourne, and Itchtucknee River, Florida.

Genus **MERGUS** Linnaeus

Mergus LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 129. Type, by subsequent designation, *Mergus castor* Linnaeus = *Mergus merganser* Linnaeus (Gray, 1840).

Mergus merganser LINNAEUS: Merganser

Mergus Merganser LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 129.

Modern form reported from Pleistocene: North Shore Channel, Chicago, Illinois.⁴¹ Late Pleistocene: Fossil Lake, Oregon.

Mergus serrator LINNAEUS: Red-breasted Merganser

Mergus Serrator LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 129.

Modern form reported from late Pleistocene: Fossil Lake, Oregon.

³⁹ Shufeldt's record from Fossil Lake, Oregon, is based on an erroneous identification. See Howard, Carnegie Inst. Washington Publ. 551, Jan. 25, 1946, p. 176.

⁴⁰ See Wetmore, Condor, vol. 57, No. 3, 1955, p. 189.

⁴¹ Formerly recorded as *Mergus serrator*; see Wetmore, Wilson Bull., 1948, p. 240.

Order FALCONIFORMES: VULTURES, HAWKS, and FALCONS

Suborder CATHARTAE: NEW WORLD VULTURES

Superfamily NEOCATHARTOIDEA: NEOCATHARTES

Family NEOCATHARTIDAE: NEOCATHARTES

Genus NEOCATHARTES Wetmore

Neocathartes WETMORE, Auk, vol. 67, No. 2, April 1950, p. 235. Type, by original designation, *Eocathartes grallator* Wetmore.

***Neocathartes grallator* (WETMORE)**

Eocathartes grallator WETMORE, Ann. Carnegie Mus., vol. 30, May 24, 1944, p. 58, pls. 1-5, figs. 1-10.

Upper Eocene (Upper Washakie beds): Sand wash one-half mile north of Dobe Town Road crossing, Sweetwater County, Wyoming.

Superfamily CATHARTOIDEA: NEW WORLD VULTURES

Family CATHARTIDAE: NEW WORLD VULTURES

Genus CATHARTES Illiger

Cathartes ILLIGER, Prodromus, 1811, p. 236. Type, by subsequent designation, *Vultur aura* Linnaeus (Vigors, 1825).

***Cathartes aura* (LINNAEUS): Turkey Vulture ⁴²**

Vultur aura LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 86.

Modern form reported from Pleistocene: Seminole Field, Pinellas County,⁴³ Melbourne, and cavern deposits near Lecanto, Florida. Late Pleistocene: Potter Creek and Samwel caves, Shasta County, Hawver Cave, Eldorado County, Carpinteria, Santa Barbara County, McKittrick, Kern County, Rancho La Brea, Los Angeles, and San Pedro (Palos Verdes sand, lumberyard locality), Los Angeles County, California.

Genus CORAGYPS Geoffroy

Coragyps GEOFFROY Ms in Le Maout, Hist. Nat. Oiseaux, 1853, p. 66. Type, by monotypy, *Vultur urubu* Vieillot = *Vultur atratus* Bechstein.

⁴² Wetmore, Smithsonian Misc. Coll., vol. 85, No. 2, Apr. 13, 1931, pp. 4, 6, 7, 23-24, has recorded the small Mexican turkey vulture, *Cathartes aura aura*, from Seminole Field, Pinellas County, Florida. Other reports of this species are mainly of the larger type, of which two races, *septentrionalis* and *teter*, are at present recognized in the United States.

⁴³ Recorded from Vero, stratum 2, erroneously by Shufeldt, 9th Ann. Rep. Florida State Geol. Surv., 1917, p. 36. The record from Vero (stratum 3) is of Recent age according to Cooke, Florida Geol. Surv. Bull. 29, 1945, pp. 306-307.

***Coragyps atratus* (BECHSTEIN): Black Vulture**

Vultur atratus BECHSTEIN, in John Latham's allg. Uebers Vogel, Bd. 1, Anh., 1793, p. 655.

Modern form reported from Pleistocene: Seminole Field, Pinellas County, and cavern deposits near Lecanto, Florida. Quaternary (probably Recent): Rocky Arroyo, New Mexico.

***Coragyps occidentalis* (MILLER)⁴⁴**

Catharista occidentalis L. H. MILLER, Univ. California Publ., Bull. Dept. Geol., vol. 5, No. 21, Sept. 10, 1909, p. 306.

Pleistocene: San Josecito Cavern, Aramberri, Nuevo León.⁴⁵ Late Pleistocene: Potter Creek and Samwel caves, Shasta County; Carpinteria, Santa Barbara County; McKittrick, Kern County; and Rancho La Brea, Los Angeles, California.

Genus PHASMAGYPS Wetmore

Phasmagyps WETMORE, Proc. Colorado Mus. Nat. Hist., vol. 7, No. 2, July 15, 1927, p. 3. Type, by monotypy, *Phasmagyps patritus* Wetmore.

***Phasmagyps patritus* WETMORE**

Phasmagyps patritus WETMORE, Proc. Colorado Mus. Nat. Hist., vol. 7, No. 2, July 15, 1927, p. 3, figs. 1-4.

Lower Oligocene (Chadron formation): Horsetail Creek, Weld County, Colorado.

Genus PALAEOGYPS Wetmore

Palaeogyps WETMORE, Proc. Colorado Mus. Nat. Hist., vol. 7, No. 2, July 15, 1927, p. 5. Type, by monotypy, *Palaeogyps prodromus* Wetmore.

***Palaeogyps prodromus* WETMORE**

Palaeogyps prodromus WETMORE, Proc. Colorado Mus. Nat. Hist., vol. 7, No. 2, July 15, 1927, p. 5, figs. 5-14.

Lower Oligocene (Chadron formation): Horsetail Creek, Weld County, Colorado.

⁴⁴ *Coragyps shastensis* (Miller) is a synonym according to Miller, Condor, 1941, pp. 140-141.

⁴⁵ Recorded also from deposits that may be late Pleistocene or early Recent in Pit 10 at Rancho La Brea (Howard, H., and Miller, A. H., Carnegie Inst. Washington Publ. 514, 1939, p. 43), Conkling Cavern, Pyramid Peak, Organ Mountains, Dona Ana County, New Mexico (Howard, H., and Miller, A. H., Condor, vol. 35, Jan. 15, 1933, pp. 15, 17), and from Smith Creek Cave, 34 miles north of Baker, White Pine County, Nevada (Howard, H., Condor, vol. 37, July 15, 1935, pp. 206-207).

Genus GYMNOGYPS Lesson

Gymnogyps LESSON, Écho du Monde Savant, ser. 2, vol. 6, Dec. 8, 1842, col. 1037. Type, by monotypy, *Vultur californianus* Shaw.

Gymnogyps amplus MILLER⁴⁶

Gymnogyps amplus L. H. MILLER, Univ. California Publ., Bull. Dept. Geol., vol. 6, No. 16, Oct. 28, 1911, p. 390, fig. 2.

Pleistocene: Sarasota and Seminole Field, Pinellas County, Florida; San Josecito Cave, Aramberri, Nuevo León. Late Pleistocene: Samuel Cave (type locality) and Stone Man Cave, Shasta County; Carpinteria, McKittrick, and Rancho La Brea, Los Angeles, California. Quaternary (probably Recent): Rocky Arroyo, New Mexico.

Genus BREAGYPS Miller and Howard

Breagyps L. H. MILLER and H. HOWARD, Publ. Univ. California at Los Angeles, Biol. Sci., vol. 9, Feb. 18, 1938, p. 171. Type, by original designation, *Vultur clarki* Miller = *Sarcorhamphus clarki* Miller.

Breagyps clarki (MILLER)

Sarcorhamphus clarki L. H. MILLER, Univ. California Publ., Bull. Dept. Geol., vol. 6, No. 1, Nov. 28, 1910, p. 11, figs. 3a, 3b.

Late Pleistocene: Rancho La Brea, Los Angeles, California. Quaternary (probably late Pleistocene): Smith Creek Cave, 34 miles north of Baker, White Pine County, Nevada.

Genus SARCORAMPHUS Duméril

Sarcoramphus DUMÉRIL, Zoöl. Anal., 1806, p. 32. Type, by subsequent designation, *Vultur papa* Linnaeus (Vigors, 1825).

Sarcoramphus kernense (MILLER)

Vultur kernensis L. H. MILLER, Condor, vol. 33, Mar. 18, 1931, p. 70, fig. 16.

Pliocene: Pozo Creek, Kern River Divide, Kern County, about 9 miles northeast of Bakersfield, California.

Family TERATORNITHIDAE: TERATORNITHES

Genus TERATORNIS Miller

Teratornis, L. H. MILLER, Univ. California Publ., Bull. Dept. Geol., vol. 5, No. 21, Sept. 10, 1909, p. 307. Type, by monotypy, *Teratornis merriami* Miller.

⁴⁶ Fisher, Pacific Science, vol. 1, No. 4, October 1947, p. 227, finds that all fossil material from western North America formerly placed under the living *Gymnogyps californianus* is properly assigned to the present bird, which is so slightly differentiated as to be considered the direct Pleistocene progenitor of the modern form. The remaining records, from Florida and Nuevo León, are placed under *amplus* on the basis of probability.

Teratornis merriami MILLER

Teratornis merriami L. H. MILLER, Univ. California Publ., Bull. Dept. Geol., vol. 5, No. 21, Sept. 10, 1909, p. 307, text figs. 1-9.

Pleistocene: Seminole Field, Pinellas County, and Bradenton, Florida; San Josecito Cave, Aramberri, Nuevo León. Late Pleistocene: Rancho La Brea (type locality),⁴⁷ Los Angeles, McKittrick, Kern County, and Carpinteria, Santa Barbara County, California.

Teratornis incredibilis HOWARD

Teratornis incredibilis HOWARD, Bull. Southern California Acad. Sci., vol. 51, pt. 2, 1952, p. 51, pl. 10, figs. 1-2.

Quaternary (probably late Pleistocene): Smith Creek Cave, 34 miles north of Baker, White Pine County, Nevada.

Genus CATHARTORNIS Miller⁴⁸

Cathartornis L. H. MILLER, Univ. California Publ., Bull. Dept. Geol., vol. 6, No. 1, Nov. 28, 1910, p. 14. Type, by monotypy, *Cathartornis gracilis* Miller.

Cathartornis gracilis MILLER

Cathartornis gracilis L. H. MILLER, Univ. California Publ., Bull. Dept. Geol., vol. 6, No. 1, Nov. 28, 1910, p. 14, figs. 4a, 4b.

Late Pleistocene: Rancho La Brea, Los Angeles, California.

Suborder FALCONES: SECRETARY-BIRDS, HAWKS, and FALCONS

Superfamily FALCONOIDEA: HAWKS, FALCONS, and ALLIES

Family ACCIPITRIDAE: HAWKS, OLD WORLD VULTURES, and HARRIERS

Subfamily AEGYPIINAE: OLD WORLD VULTURES

Genus PALAEOBORUS Coues

Palacoborus COUES, Key North Amer. Birds, ed. 2, 1884, p. 822. Type, by original designation, *Cathartes umbrosus* Cope.

Palaeoborus umbrosus (COPE)⁴⁹

Cathartes umbrosus COPE, Proc. Acad. Nat. Sci. Philadelphia, vol. 26, Oct. 20, 1874, p. 151.

Pliocene: North of Pojauque, New Mexico.

⁴⁷ Recorded also from early Recent deposits in Pit 10, at Rancho La Brea (Howard, H., and Miller, A. H., Carnegie Inst. Washington Publ. 514, 1939, p. 43).

⁴⁸ Allocated to Teratornithidae by Miller, L. H., and Howard, H., Publ. Univ. California at Los Angeles, Biol. Sci., vol. 9, Feb. 18, 1938, pp. 169-170, 173.

⁴⁹ Placed in Aegyptiinae by Howard, Carnegie Inst. Washington Publ. 349, 1932, pp. 45, 70-73, 75, 76.

Palaeoborus howardae WETMORE

Palaeoborus howardae WETMORE, Proc. U. S. Nat. Mus., vol. 84, No. 3, 1936, p. 73, fig. 13.

Miocene: Dawes County, Nebraska.

Palaeoborus rosatus MILLER and COMPTON

Palaeoborus rosatus A. H. MILLER and L. V. COMPTON, Condor, vol. 41, No. 4, July 15, 1939, p. 156, fig. 34B.

Lower Miocene (Rosebud formation): Flint Hill, 9 miles west-southwest of Martin, Bennett County, South Dakota.

Genus NEOGYPS Miller

Neogyphs L. H. MILLER, Univ. California Publ., Bull. Dept. Geol., vol. 9, No. 9, Mar. 10, 1916, p. 108. Type, by monotypy, *Neogyphs errans* Miller.

Neogyphs errans MILLER

Neogyphs errans L. H. MILLER, Univ. California Publ., Bull. Dept. Geol., vol. 9, No. 9, Mar. 10, 1916, p. 108, fig. 2.

Late Pleistocene: Rancho La Brea (type locality),⁵⁰ Los Angeles, Carpinteria, Santa Barbara County, and McKittrick, Kern County, California; San Josecito Cave, Aramberri, Nuevo León. Quaternary: Smith Creek Cave, 34 miles north of Baker, White Pine County, Nevada.

Genus NEOPHRONTOPS Miller

Neophrontops L. H. MILLER, Univ. California Publ., Bull. Dept. Geol., vol. 9, No. 9, Mar. 10, 1916, p. 106. Type, by monotypy, *Neophrontops americanus* Miller.

Neophrontops americanus MILLER

Neophrontops americanus L. H. MILLER, Univ. California Publ., Bull. Dept. Geol., vol. 9, No. 9, Mar. 10, 1916, p. 106, fig. 1.

Late Pleistocene: Rancho La Brea (type locality),⁵¹ Los Angeles, Carpinteria, and McKittrick, California; San Josecito Cave, Aramberri, Nuevo León.

Neophrontops dakotensis COMPTON

Neophrontops dakotensis COMPTON, Amer. Journ. Sci., ser. 5, vol. 30, October 1935, p. 344, fig. 1.

Lower Pliocene: Big Spring Canyon, 15 miles southwest of Martin, Bennett County, South Dakota.

⁵⁰ Recorded also from early Recent deposits in Pit 10 at this site (Howard, H., and Miller, A. H., Carnegie Inst. Washington Publ. 514, 1939, p. 43).

⁵¹ Recorded also from early Recent deposits in Pit 10 at this site (Howard, H., and Miller, A. H., Carnegie Inst. Washington Publ. 514, 1939, p. 43).

Neophrontops vetustus WETMORE

Neophrontops vetustus WETMORE, Condor, vol. 45, No. 6, Dec. 8, 1943, p. 229, fig. 62.

Middle Miocene (Sheep Creek beds): Stonehouse Draw Quarry, Sioux County, Nebraska.

Subfamily ELANINAE: WHITE-TAILED KITES

Genus **ELANUS** Savigny

Elanus SAVIGNY, Descr. Égypte, vol. 1, 1809, pp. 69, 97. Type, by monotypy, *Elanus caesius* Savigny = *Falco caeruleus* Desfontaines.

Elanus leucurus (VIEILLOT): White-tailed Kite

Milvus leucurus VIEILLOT, Nouv. Dict. Hist. Nat., nouv. éd., vol. 20, May 1818, p. 563 [errone = 556].

Modern form reported from Pleistocene: San Josecito Cave, Aramberri, Nuevo León. Late Pleistocene: Rancho La Brea, Los Angeles, California.

Subfamily MILVINAE: TRUE KITES

Genus **PROICTINIA** Shufeldt

Proictinia SHUFELDT, Bull. Amer. Mus. Nat. Hist., vol. 32, art. 16, Aug. 4, 1913, p. 301. Type, by monotypy, *Proictinia gilmorei* Shufeldt.

Proictinia efferata WETMORE

Proictinia efferata WETMORE, Bull. Amer. Mus. Nat. Hist., vol. 48, art. 12, Dec. 3, 1923, p. 504, figs. 19-20.

Lower Miocene (Lower Harrison beds): Agate Fossil Quarry, Sioux County, Nebraska.

Proictinia gilmorei SHUFELDT

Proictinia gilmorei SHUFELDT, Bull. Amer. Mus. Nat. Hist., vol. 32, art. 16, Aug. 4, 1913, p. 301, pl. 55, fig. 27.

Lower Pliocene (Ogallala formation): Long Island, Phillips County, Kansas.

Subfamily ACCIPITRINAE: BIRD HAWKS

Genus **ACCIPITER** Brisson

Accipiter BRISSON, Orn., 1760, vol. 1, p. 28; vol. 6, p. 310. Type, by tautonymy, *Accipiter* Brisson = *Falco nisus* Linnaeus.

Accipiter gentilis (LINNAEUS): Goshawk

Falco gentilis LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 89.

Modern form reported from late Pleistocene: Carpinteria, Santa Barbara County, and Rancho La Brea, Los Angeles, California.

Accipiter striatus velox (WILSON): Sharp-shinned Hawk

Falco velox WILSON, Amer. Orn., vol. 5, 1812, p. 116, pl. 45, fig. 1.

Modern form reported from late Pleistocene: Samwel Cave, Shasta County, Carpinteria, Santa Barbara County, and Rancho La Brea, Los Angeles, California.

Accipiter cooperii (BONAPARTE): Cooper's Hawk

Falco Cooperii BONAPARTE, Amer. Orn., vol. 2, 1828, p. 1, pl. 10, fig. 1.

Modern form reported from late Pleistocene: McKittrick, Kern County, Carpinteria, Santa Barbara County, and Rancho La Brea, Los Angeles, California.

Subfamily BUTEONINAE: BUZZARDS and EAGLES**Genus BUTEO Lacépède**

Buteo LACÉPÈDE, Tabl. Ois., 1799, p. 4. Type, by tautonymy, *Falco buteo* Linnaeus.

Buteo jamaicensis (GMELIN): Red-tailed Hawk

Falco jamaicensis GMELIN, Syst. Nat., vol. 1, pt. 1, 1788, p. 266.

Modern form reported from late Pleistocene: Potter Creek Cave, Shasta County, McKittrick, Carpinteria, and Rancho La Brea, Los Angeles, California. Pleistocene: Seminole Field, Pinellas County, Venice, and Melbourne (stratum 2), Florida.

Buteo lineatus (GMELIN): Red-shouldered Hawk

Falco lineatus GMELIN, Syst. Nat., vol. 1, pt. 1, 1788, p. 268.

Modern form reported from Pleistocene: Seminole Field, Pinellas County, Venice, and Melbourne, Florida. Late Pleistocene: Carpinteria, Santa Barbara County, California.

Buteo platypterus (VIEILLOT): Broad-winged Hawk

Sparvius platypterus VIEILLOT, Tabl. Encycl. Méth. Orn., vol. 3, 1823, p. 1273.

Modern form reported from Pleistocene: Seminole Field, Pinellas County, Florida.

Buteo swainsoni BONAPARTE: **Swainson's Hawk**

Buteo swainsoni BONAPARTE, Geogr. and Comp. List, 1838, p. 3.

Modern form reported from late Pleistocene: McKittrick, Kern County, and Rancho La Brea, Los Angeles, California.

Buteo lagopus (PONTOPPIDAN): **Rough-legged Hawk**

Falco lagopus PONTOPPIDAN, Danske Atlas, 1763, p. 616.

Modern form reported from late Pleistocene: Rancho La Brea, Los Angeles, California.

Buteo regalis (GRAY): **Ferruginous Hawk**

Archibuteo regalis G. R. GRAY, Genera of Birds, vol. 1, pt. 1, May 1844, pl. 6.

Modern form reported from late Pleistocene: Hawver Cave, Eldorado County, Rancho La Brea, Los Angeles, Carpinteria, Santa Barbara County, and McKittrick, Kern County, California.

Buteo fuscescens (VIEILLOT): **Buzzard Eagle**

Spizaetus fuscescens VIEILLOT, Nouv. Dict. Hist. Nat., nouv. éd., vol. 32, September 1819, p. 55.

Modern form⁵² reported from late Pleistocene: Baños de Ciego Montero, Santa Clara Province, Cuba.

Buteo antecursor WETMORE

Buteo antecursor WETMORE, Bull. Mus. Comp. Zoöl., vol. 75, October 1933, p. 298, figs. 1-5.

Oligocene (Brule formation): Near Torrington, Goshen County, Wyoming.

Buteo grangeri WETMORE and CASE

Buteo grangeri WETMORE and CASE, Contr. Mus. Pal. Univ. Michigan, vol. 4, No. 8, Jan. 15, 1934, p. 129, 1 pl.

Middle Oligocene (Brule formation, Oreodon beds): Big Badlands of Pass Creek, Washabaugh County, South Dakota.

Buteo fluviaticus MILLER and SIBLEY

Buteo fluviaticus A. H. MILLER and C. G. SIBLEY, Condor, vol. 44, No. 1, Jan. 15, 1942, p. 39, fig. 12.

Middle Oligocene (Brule formation, Oreodon beds): Owl Creek, 6 miles east of Carr, Weld County, Colorado.

⁵² Formerly called *Buteo melanoleucus* (Vieillot). The modern range extends from the mountains of Venezuela and Colombia, south through Ecuador and Perú to Chile, and from southeastern Brazil and Paraguay to Tierra del Fuego.

Buteo typhoius WETMORE

Buteo typhoius WETMORE, Bull. Amer. Mus. Nat. Hist., vol. 48, art. 12, Dec. 3, 1923, p. 489, figs. 3-5.

Lower Miocene (Lower Harrison beds) ; Upper Miocene ⁵³ (Lower Snake Creek beds, type locality) : south of Agate, Sioux County, Nebraska.

Buteo ales (WETMORE)

Geranoaëtus ales WETMORE, Ann. Carnegie Mus., vol. 16, No. 4, Apr. 10, 1926, p. 403, pl. 38, figs. 1-5.

Lower Miocene (Lower Harrison beds) : Quarry No. 2, Agate Springs Fossil Quarries, Sioux County, Nebraska.

Buteo contortus (WETMORE)

Geranoaëtus contortus WETMORE, Bull. Amer. Mus. Nat. Hist., vol. 48, art. 12, Dec. 3, 1923, p. 492, figs. 6-9.

Upper Miocene ⁵³ (Lower Snake Creek beds) : Sinclair Draw (type locality) and Olcott Hill, Sioux County, Nebraska.

Buteo dananus (MARSH)

Aquila danana MARSH, Amer. Journ. Sci., ser. 3, vol. 2, August 1871, p. 125.

Lower Pliocene (Upper Snake Creek beds) : Loup Fork River, Nebraska.

Buteo conterminus (WETMORE)

Geranoaëtus conterminus WETMORE, Bull. Amer. Mus. Nat. Hist., vol. 48, art. 12, Dec. 3, 1923, p. 497, figs. 11-13.

Lower Pliocene (Upper Snake Creek beds) : 20 miles south of Agate, Sioux County, Nebraska.

Genus PARABUTEO Ridgway

Parabuteo RIDGWAY, in Baird, Brewer, and Ridgway, Hist. North Amer. Birds, vol. 3, 1874, p. 250. Type, by monotypy, *Buteo harrisi* Audubon.

Parabuteo unicinctus (TEMMINCK) : Harris' Hawk

Falco unicinctus TEMMINCK, Planch. Col. Ois., livr. 53, Dec. 25, 1824, pl. 313.

Modern form reported from Pleistocene: San Josecito Cave, Aramberri, Nuevo León.

⁵³ Possibly early Pliocene; cf. Cook, H. J., and Cook, M. C., Nebraska Geol. Surv., Paper No. 5, 1933, p. 42.

Genus **CALOHIERAX** Wetmore

Calohierax WETMORE, Bull. Mus. Comp. Zoöl., vol. 80, No. 12, October 1937, p. 428. Type, by original designation, *Calohierax quadratus* Wetmore.

Calohierax quadratus WETMORE

Calohierax quadratus WETMORE, Bull. Mus. Comp. Zoöl., vol. 80, No. 12, October 1937, p. 429, figs. 1-3.

Recent (extinct):⁵⁴ Cave deposits on Great Exuma Island, Bahama Islands.

Genus **MIOHIERAX** Howard

Miohierax HOWARD, Condor, vol. 46, No. 5, Sept. 27, 1944, p. 236. Type, by original designation, *Miohierax stocki* Howard.

Miohierax stocki HOWARD

Miohierax stocki HOWARD, Condor, vol. 46, No. 5, Sept. 27, 1944, p. 236, fig. 40.

Late Lower Miocene (Tick Canyon formation): Near head of Vasquez Canyon, Los Angeles County, California.

Genus **HYPOMORPHNUS** Cabanis⁵⁵

Hypomorphnus CABANIS, Arch. Naturg., vol. 10, Bd. 1, 1844, p. 263. Type, by original designation, *Falco urubitinga* Linnaeus.

Hypomorphnus enectus (WETMORE)

Urubitinga enecta WETMORE, Bull. Amer. Mus. Nat. Hist., vol. 48, art. 12, Dec. 3, 1923, p. 500, figs. 14-18.

Middle Miocene (Lower Sheep Creek beds): 20 miles south of Agate, Sioux County, Nebraska.

Hypomorphnus sodalis (SHUFELDT)⁵⁶

Aquila sodalis SHUFELDT, Amer. Nat., vol. 25, No. 297, September 1891, p. 821.

Late Pleistocene: Fossil Lake, Oregon.

Genus **TITANOHIERAX** Wetmore

Titanohierax WETMORE, Bull. Mus. Comp. Zoöl., vol. 80, No. 12, October 1937, p. 430. Type, by original designation, *Titanohierax gloveralleni* Wetmore.

⁵⁴ Included here since it has not been found in living form, being known only from its bones.

⁵⁵ For the use of *Hypomorphnus* to replace *Urubitinga* see Peters, Check-list of the birds of the world, vol. 1, 1931, p. 244.

⁵⁶ Generic allocation questionable. See Howard, Carnegie Inst. Washington Publ. 551, Jan. 25, 1946, pp. 177-178.

***Titanohierax gloveralleni* WETMORE**

Titanohierax gloveralleni WETMORE, Bull. Mus. Comp. Zoöl., vol. 80, No. 12, October 1937, p. 431, figs. 4-9.

Recent (extinct): ⁵⁷ Cave deposits on Great Exuma Island, Bahama Islands.

Genus BUTEOGALLUS Lesson

Buteogallus LESSON, Traité d'Orn., livr. 2, 1830, p. 83. Type, by monotypy, *Buteogallus cathartoides* Lesson = *Falco aequinoctialis* Gmelin.

***Buteogallus milleri* (HOWARD) ⁵⁸**

Urubitinga milleri HOWARD, Carnegie Inst. Washington Publ. 429, October 1932, p. 25, pl. 2, figs. 3-3a, pl. 3, fig. 2.

Late Pleistocene: Hawver Cave, Eldorado County, California.

***Buteogallus fragilis* (MILLER) ⁵⁸**

Geranoaëtus fragilis L. H. MILLER, Univ. California Publ., Bull. Dept. Geol., vol. 6, No. 12, Oct. 9, 1911, p. 315, figs. 5a, 5b.

Late Pleistocene: McKittrick, Kern County, Rancho La Brea (type locality), ⁵⁹ Los Angeles, and Carpinteria, Santa Barbara County, California.

Genus WETMOREGYPS Miller

Wetmoregyps L. H. MILLER, Condor, vol. 30, No. 4, July 16, 1928, p. 255. Type, by original designation, *Morphnus daggetti* Miller.

***Wetmoregyps daggetti* (MILLER)**

Morphnus daggetti L. H. MILLER, Condor, vol. 17, No. 5, Oct. 10, 1915, p. 179, fig. 63.

Pleistocene: San Josecito Cave, Aramberri, Nuevo León. Late Pleistocene: Rancho La Brea (type locality), Los Angeles, and Carpinteria, Santa Barbara County, California.

Genus MORPHNUS Dumont

Morphnus DUMONT, Dict. Sci. Nat., vol. 1, Suppl., October 1816, p. 88. Type, by subsequent designation, *Falco guianensis* Daudin (Chubb, 1916).

⁵⁷ Included here since it has not been found in living form, being known only from its bones.

⁵⁸ Referred to this genus by Howard, Carnegie Inst. Washington Publ. 551, Jan. 25, 1946, p. 177.

⁵⁹ Recorded also from early Recent deposits in Pit 10 at Rancho La Brea (Howard, H., and Miller, A. H., Carnegie Inst. Washington Publ. 514, 1939, p. 43). And from late Pleistocene or early Recent deposits in Shelter Cave, Pyramid Peak, Organ Mountains, Dona Ana County, New Mexico, by Howard, H., and Miller, A. H., Condor, vol. 35, 1933, pp. 16, 17.

Morphnus woodwardi MILLER

Morphnus woodwardi L. H. MILLER, Univ. California Publ., Bull. Dept. Geol., vol. 6, No. 12, Oct. 9, 1911, p. 312, figs. 3a, 3b.

Late Pleistocene: Rancho La Brea, Los Angeles, California.⁶⁰

Genus SPIZAËTUS Vieillot

Spizaëtus VIEILLOT, Analyse, 1816, p. 24. Type, by subsequent designation, *Falco ornatus* Daudin (Gray, 1840).

Spizaëtus grinnelli (MILLER)⁶¹

Geranoaëtus grinnelli L. H. MILLER, Univ. California Publ., Bull. Dept. Geol., vol. 6, No. 12, Oct. 9, 1911, p. 314, figs. 4a, 4b.

Pleistocene: San Josecito Cave, Aramberri, Nuevo León. Late Pleistocene: Rancho La Brea (type locality),⁶² Los Angeles, McKittrick and Carpinteria, California.

Spizaëtus willetti HOWARD

Spizaëtus willetti HOWARD, Condor, vol. 37, No. 4, July 15, 1935, p. 207, fig. 40.

Quaternary (probably late Pleistocene): Smith Creek Cave, 34 miles north of Baker, White Pine County, Nevada.

Spizaëtus pliogryps (SHUFELDT)

Aquila pliogryps SHUFELDT, Amer. Nat., vol. 25, No. 297, September 1891, p. 821.

Late Pleistocene: Fossil Lake, Oregon.

Genus PALAEASTUR Wetmore

Palaeastur WETMORE, Condor, vol. 45, No. 6, Dec. 8, 1943, p. 230. Type, by original designation, *Palaeastur atavus* Wetmore.

Palaeastur atavus WETMORE

Palaeastur atavus WETMORE, Condor, vol. 45, No. 6, Dec. 8, 1943, p. 230, fig. 63.

Lower Miocene (Lower Harrison beds); Stenomylus Quarry, about 2 miles southeast of Agate Springs fossil site, near Agate, Nebraska.

⁶⁰ Recorded also from early Recent deposits in Pit 10 at this site (Howard, H., and Miller, A. H., Carnegie Inst. Washington Publ. 514, 1939, p. 43).

⁶¹ Allocated in *Spizaëtus* by Howard, Carnegie Inst. Washington Publ. 429, 1932, pp. 33-44.

⁶² Placed in *Spizaëtus* by Howard, Carnegie Inst. Washington Publ. 551, Jan. 25, 1946, pp. 176-177.

Genus **AQUILA** Brisson ⁶³

Aquila BRISSON, Orn., 1760, vol. 1, pp. 28, 419. Type, by tautonymy, *Aquila* Brisson = *Falco chrysaëtos* Linnaeus.

Aquila chrysaëtos (LINNAEUS): **Golden Eagle**

Falco Chrysaëtos LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 88.

Modern form reported from Pleistocene: San Josecito Cave, Aramberri, Nuevo León. Late Pleistocene: Fossil Lake, Oregon; Rancho La Brea,⁶⁴ Los Angeles, Carpinteria, McKittrick, and near Manix, San Bernardino County, California.

Genus **HALIAEETUS** Savigny

Haliaeetus SAVIGNY, Descr. Égypte, Ois., vol. 1, 1809, pp. 68, 85. Type, by monotypy, *Haliaeetus nisus* Savigny = *Falco albicilla* Linnaeus.

Haliaeetus leucocephalus (LINNAEUS): **Bald Eagle**

Falco leucocephalus LINNAEUS, Syst. Nat., ed. 12, vol. 1, 1766, p. 124.

Modern form reported from Pleistocene: Seminole Field, Pinellas County, Venice, Melbourne, and cavern deposits near Lecanto, Florida; Niobrara River, near Peters, Sheridan County, Nebraska. Late Pleistocene: Fossil Lake, Oregon; Carpinteria, McKittrick, Rancho La Brea, Los Angeles, and San Pedro (Palos Verdes sand), Los Angeles County, California.

Subfamily **PALAEOPLANCINAE**: **PALAEOPLANCUS**Genus **PALAEOPLANCUS** Wetmore

Palaeoplancus WETMORE, Smithsonian Misc. Coll., vol. 87, No. 19, Dec. 26, 1933, p. 1. Type, by original designation, *Palaeoplancus sternbergi* Wetmore.

Palaeoplancus sternbergi WETMORE

Palaeoplancus sternbergi WETMORE, Smithsonian Misc. Coll., vol. 87, No. 19, Dec. 26, 1933, p. 12, figs. 1-19.

Middle Oligocene (Brule formation, Upper Oreodon beds): East side of Plum Creek, Niobrara County, Wyoming.

⁶³ *Aquila ferox* Shufeldt proves to be a mammal. See Wetmore, Amer. Mus. Nov., No. 680, Dec. 4, 1933, pp. 1-2.

⁶⁴ Howard, Auk, vol. 64, April 1947, pp. 287-291, finds that the abundant material from Rancho La Brea indicates a bird with longer wing, shorter leg, and larger skull than the living population.

Subfamily CIRCINAE: HARRIERS

Genus CIRCUS Lacépède

Circus LACÉPÈDE, Tabl. Ois., 1799, p. 4. Type, by subsequent designation, *Falco aeruginosus* Linnaeus (Lesson, 1828).

Circus cyaneus (LINNAEUS): Marsh Hawk

Falco cyaneus LINNAEUS, Syst. Nat., ed. 12, vol. 1, 1766, p. 126.

Modern form reported from Pleistocene: San Josecito Cave, Aramberri, Nuevo León. Late Pleistocene: Fossil Lake, Oregon; McKittrick, and Rancho La Brea, Los Angeles, California.

Family PANDIONIDAE: OSPREYS

Genus PANDION Savigny

Pandion SAVIGNY, Descr. Égypte, Ois., vol. 1, 1809, pp. 69, 96. Type, by monotypy, *Pandion fluvialis* Savigny = *Falco haliaetus* Linnaeus.

Pandion haliaetus LINNAEUS: Osprey

Falco Haliaetus LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 91.

Modern form reported from Pleistocene: Melbourne (stratum 2), and Itchtucknee River, Florida.

Family FALCONIDAE: CARACARAS and FALCONS

Subfamily CARACARINAE: CARACARAS

Genus CARACARA Merrem

Caracara MERREM, in Ersch and Gruber, Allg. Encycl. Wiss. Künste, vol. 15, 1826, p. 159. Type, by subsequent designation, *Falco plancus* Miller (Hellmayr and Conover, 1949).

Caracara prelutosus prelutosus (HOWARD)

Polyborus prelutosus HOWARD, Carnegie Inst. Washington Publ. 487, July 7, 1938, p. 226, pls. 1-3.

Pleistocene: Seminole Field, Pinellas County, and Melbourne, Florida. Late Pleistocene: McKittrick, Kern County; Carpinteria, Santa Barbara County; and Rancho La Brea (type locality), Los Angeles, California.⁶⁵

⁶⁵ Recorded also from early Recent deposits at this site (Howard, H., and Miller, A. H., Carnegie Inst. Washington Publ. 514, 1939, p. 43) and from Quaternary deposits in Conkling Cavern, Organ Mountains, New Mexico.

Caracara prelutosus grinnelli (HOWARD)

Polyborus prelutosus grinnelli HOWARD, Condor, vol. 42, No. 1, Jan. 19, 1940, p. 41.

Pleistocene: San Josecito Cave, Aramberri, Nuevo León.

Caracara latebrosus (WETMORE)

Polyborus latebrosus WETMORE, Proc. Biol. Soc. Washington, vol. 33, Dec. 30, 1920, p. 77, pl. 2, figs. 5, 6.

Recent (extinct): ⁶⁶ Cave deposits in Cueva Toraño, near Utuado, Puerto Rico.

Subfamily FALCONINAE: FALCONS

Genus **FALCO** Linnaeus

Falco LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 88. Type, by subsequent designation, *Falco subbuteo* Linnaeus (A. O. U. Comm., 1886).

Subgenus **HIEROFALCO** Cuvier

Hierofalco CUVIER, Règne Animal, vol. 1, 1817 (Dec. 7, 1816), p. 312. Type, by monotypy, *Falco candicans* Gmelin.

Falco mexicanus SCHLEGEL: **Prairie Falcon**

Falco mexicanus SCHLEGEL, Abh. Geb. Zool. Vergl. Anat., Heft 3, 1851, p. 15.

Modern form reported from Pleistocene: San Josecito Cave, Aramberri, Nuevo León. Late Pleistocene: McKittrick, and Rancho La Brea, Los Angeles, California.

Falco swarthi MILLER

Falco swarthi L. H. MILLER, Condor, vol. 29, No. 3, May 15, 1927, p. 152, fig. 54.

Late Pleistocene: McKittrick, California.

Falco oregonus HOWARD

Falco oregonus H. HOWARD, Carnegie Inst. Washington Publ. 551, Jan. 25, 1946, p. 178, pl. 1, figs. 2, 3.

Late Pleistocene: Fossil Lake, Oregon.

Subgenus **RHYNCHODON** Nitzsch

Rhynchodon NITZSCH, Obs. Avium Art. Carot. Comm., 1829, p. 20. Type, by subsequent designation, *Falco peregrinus* Tunstall (A. O. U. Comm., 1886).

⁶⁶ Included here since it has not been found in living form, being known only from bones.

Falco peregrinus TUNSTALL: Peregrine Falcon

Falco Peregrinus TUNSTALL, Orn. Brit., 1771, p. 1.

Modern form reported from Late Pleistocene: Potter Creek Cave, Shasta County, McKittrick, and Rancho La Brea, Los Angeles, California.

Subgenus TINNUNCULUS Vieillot

Tinnunculus VIEILLOT, Ois. Amér. Sept., vol. 1, 1807, p. 39. Type, by subsequent designation, *Falco columbarius* Linnaeus (Walden, 1872).

Falco columbarius LINNAEUS: Pigeon Hawk

Falco columbarius LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 90.

Modern form reported from late Pleistocene: McKittrick, and Rancho La Brea, Los Angeles, California.

Falco ramenta WETMORE

Falco ramenta WETMORE, Proc. U. S. Nat. Mus., vol. 84, Nov. 3, 1936, p. 75, fig. 14.

Miocene (Sheep Creek formation): Dawes County, Nebraska.

Subgenus CERCHNEIS Boie

Cerchneis BOIE, Isis von Oken, vol. 19, Heft 10, October 1826, col. 970. Type, by monotypy, *Falco rupicolus* Daudin.

Falco sparverius LINNAEUS: Sparrow Hawk

Falco sparverius LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 90.

Modern form reported from Pleistocene: Cavern deposits near Lecanto, Florida; San Josecito Cavern, Aramberri, Nuevo León. Late Pleistocene: Samwel and Potter Creek caves, Shasta County, McKittrick, Carpinteria, and Rancho La Brea, Los Angeles, San Pedro (Palos Verdes sand), Los Angeles County, California.

Order GALLIFORMES: MEGAPODES, CURASSOWS, PHEASANTS,
and HOATZINS

Suborder GALLI: MEGAPODES, CURASSOWS, GROUSE, and PHEASANTS

Superfamily CRACOIDEA: MEGAPODES, CURASSOWS, and GUANS

Family GALLINULOIDIDAE: GALLINULOIDES

Genus GALLINULOIDES Eastman

Gallinuloides EASTMAN, Geol. Mag., February 1900, p. 54. Type, by monotypy, *Gallinuloides wyomingensis* Eastman.

Gallinuloides wyomingensis EASTMAN

Gallinuloides wyomingensis EASTMAN, Geol. Mag., n. s., vol. 7, pt. 4, No. 2, February 1900, p. 54, pl. 4.

Middle Eocene (Green River formation): Fossil (type locality), and Henry's Fork, Wyoming.

Family CRACIDAE: CURASSOWS, GUANS, and CHACHALACAS**Genus ORTALIS** Merrem

Ortalida (accusative case) = *Ortalis* (nominative) MERREM, Avium Rar. Icones et Descrip., vol. 2, 1786, p. 40. Type, by original designation, *Phasianus motmot* Linnaeus.

Ortalis phengites WETMORE

Ortalis phengites WETMORE, Bull. Amer. Mus. Nat. Hist., vol. 48, art. 12, Dec. 3, 1923, p. 487, figs. 1-2.

Lower Pliocene (Upper Snake Creek beds): South of Agate, Sioux County, Nebraska.

Ortalis tantala WETMORE

Ortalis tantala WETMORE, Condor, vol. 35, No. 2, Mar. 15, 1933, p. 64, figs. 10-14.

Lower Miocene (Lower Harrison beds): Carnegie Hill, Sioux County, Nebraska.

Ortalis pollicaris MILLER

Ortalis pollicaris A. H. MILLER, Univ. California Publ., Bull. Dept. Geol. Sci., vol. 27, No. 4, June 22, 1944, p. 91, fig. 5.

Lower Miocene (Rosebud formation): Flint Hill, 9 miles west-southwest of Martin, Bennett County, South Dakota.

Genus BOREORTALIS Brodkorb

Boreortalis BRODKORB, Wilson Bull., vol. 66, No. 3, September (Oct. 29), 1954, p. 180. Type, by original designation, *Boreortalis laesslei* Brodkorb.

Boreortalis laesslei BRODKORB

Boreortalis laesslei BRODKORB, Wilson Bull., vol. 66, No. 3, September (Oct. 29), 1954, p. 182, fig. 1 (on p. 181).

Lower Miocene (Hawthorn formation): Thomas Farm, 8 miles north of Bell, Gilchrist County, Florida.

Superfamily PHASIANOIDEA: GROUSE, QUAILS, PHEASANTS, and TURKEYS

Family TETRAONIDAE: GROUSE and PTARMIGANS

Genus DENDRAGAPUS Elliot

Dendragapus ELLIOT, Proc. Acad. Nat. Sci. Philadelphia, vol. 16, No. 1, January-February (April 23), 1864, p. 23. Type, by subsequent designation, *Tetrao obscurus* Say (Baird, Brewer, and Ridgway, 1874).

Dendragapus obscurus (SAY): Blue Grouse

Tetrao obscurus SAY, in Long, Exped. Rocky Mts., vol. 2, 1823, p. 14.

Modern form reported from late Pleistocene: Samwel and Potter Creek caves, Shasta County, California.

Dendragapus lucasi (SHUFELDT)⁶⁷

Pediocates lucasi SHUFELDT, Auk, vol. 8, No. 4, October 1891, p. 367.

Late Pleistocene: Fossil Lake, Oregon.

Dendragapus nanus (SHUFELDT)⁶⁷

Pediocates nanus SHUFELDT, Amer. Nat., vol. 25, No. 297, September 1891, p. 821.

Late Pleistocene: Fossil Lake, Oregon.

Genus BONASA Stephens

Bonasa STEPHENS, in Shaw, Gen. Zool., vol. 9, pt. 2, 1819, p. 298. Type, by subsequent designation, *Tetrao umbellus* Linnaeus (A. O. U. Committee, 1886).

Bonasa umbellus (LINNAEUS): Ruffed Grouse⁶⁸

Tetrao umbellus LINNAEUS, Syst. Nat., ed. 12, vol. 1, 1766, p. 275.

Modern form reported from Pleistocene: Cave near Frankstown, Pennsylvania; Cumberland Cave, near Corriganville, Allegany County, Maryland; caves of Tennessee. Late Pleistocene: Potter Creek Cave, Shasta County, California.

Genus TYMPANUCHUS Gloger⁶⁹

Tympanuchus GLOGER, Hand- und Hilfsbuch Naturg., 1842 (pp. 1-450, 1841), p. 396. Type, by monotypy, *Tetrao cupido* Linnaeus.

⁶⁷ Assigned to *Dendragapus* by Howard, Carnegie Inst. Washington Publ. 551, Jan. 25, 1946, p. 180.

⁶⁸ *Bonasa ceres* Shufeldt, Bull. Amer. Mus. Nat. Hist., vol. 32, Aug. 4, 1913, p. 299, pl. 55, figs. 18-20, pl. 56, figs. 45-72, from the Pleistocene of the fissure beds of Arkansas is possibly a synonym. On p. 300 of the reference cited the author alludes to it as *Lagopus ceres*.

⁶⁹ Records from Fossil Lake, Oregon, formerly placed under *Tympanuchus pallidicinctus* are now referred to *Centrocerus urophasianus* and *Dendragapus lucasi*. See Howard, Carnegie Inst. Washington Publ. 551, Jan. 25, 1946, p. 179.

Tympanuchus lulli SHUFELDT

Tympanuchus lulli SHUFELDT, Trans. Connecticut Acad. Arts Sci., vol. 19, February 1915, p. 69, pl. 12, fig. 90.

? Pleistocene: ⁷⁰ Hornerstown, New Jersey.

Tympanuchus stirtoni MILLER

Tympanuchus stirtoni A. H. MILLER, Univ. California Publ., Bull. Dept. Geol. Sci., vol. 27, No. 4, June 22, 1944, p. 92, fig. 6.

Lower Miocene (Rosebud formation): Flint Hill, 9 miles west-southwest of Martin, Bennett County, South Dakota.

Genus PEDIOECETES Baird

Pedioecetes BAIRD, Rep. Expl. and Surv. R. R. Pac., vol. 9, 1858, pp. xxi, xliv. Type, by monotypy, *Tetrao phasianellus* Linnaeus.

Pedioecetes phasianellus (LINNAEUS): Sharp-tailed Grouse

Tetrao Phasianellus LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 160.

Modern form reported from late Pleistocene: Fossil Lake, Oregon.

Genus CENTROCERCUS Swainson

Centrocercus SWAINSON, in Swainson and Richardson, Fauna Bor.-Amer., vol. 2, 1831 (1832), pp. 358, 496. Type, by original designation, *Tetrao urophasianus* Bonaparte.

Centrocercus urophasianus (BONAPARTE): Sage Grouse

Tetrao urophasianus BONAPARTE, Zool. Journ., vol. 3, No. 10, April-September, 1827, p. 213.

Modern form reported from late Pleistocene: Fossil Lake, Oregon.

Genus PALAEAELECTORIS Wetmore

Palaeaelectoris WETMORE, Condor, vol. 32, No. 3, May 15, 1930, p. 152. Type, by monotypy, *Palaeaelectoris incertus* Wetmore.

Palaeaelectoris incertus WETMORE

Palaeaelectoris incertus WETMORE, Condor, vol. 32, No. 3, May 15, 1930, p. 152, figs. 51-53.

Lower Miocene (Lower Harrison beds): Agate fossil quarry, near Agate, Sioux County, Nebraska.

Genus PALAEOTETRIX Shufeldt

Palaeotetrix SHUFELDT, Amer. Nat., vol. 25, No. 297, September 1891, p. 821. Type, by monotypy, *Palaeotetrix gilli* Shufeldt.

⁷⁰ Cited in the original description as "Post-Pliocene."

Palaeotetrix gilli SHUFELDT

Palaeotetrix gilli SHUFELDT, Amer. Nat., vol. 25, No. 297, September 1891, p. 821.

Late Pleistocene: Fossil Lake, Oregon.

Genus PALAEOPHASIANUS Shufeldt

Palaeophasianus SHUFELDT, Bull. Amer. Mus. Nat. Hist., vol. 32, art. 16, Aug. 4, 1913, p. 291. Type, by monotypy, *Palaeophasianus meleagroides* Shufeldt.

Palaeophasianus meleagroides SHUFELDT

Palaeophasianus meleagroides SHUFELDT, Bull. Amer. Mus. Nat. Hist., vol. 32, art. 16, Aug. 4, 1913, p. 291, pl. 58, figs. 81-84, 86-88.

Lower Eocene (Wasatch): Elk Creek, Big Horn Basin (type locality). Eocene (Bridger): Henry's Fork, Wyoming.

Family PHASIANIDAE: QUAILS, PHEASANTS, and PEACOCKS**Subfamily ODONTOPHORINAE: AMERICAN QUAILS****Genus COLINUS** Goldfuss

Colinus GOLDFUSS, Handb. Zool., vol. 2, 1820, p. 220. Type, by monotypy, *Perdix mexicanus*, Caille de la Louisiane, Pl. Enl. 149 = *Tetrao virginianus* Linnaeus.

Colinus virginianus (LINNAEUS): Bobwhite

Tetrao virginianus LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 161.

Modern form reported from Pleistocene: Seminole Field, Pinellas County, Melbourne, and cavern deposits near Lecanto, Florida; caves of Tennessee.

Colinus hibbardi WETMORE

Colinus hibbardi WETMORE, Univ. Kansas Sci. Bull., vol. 30, pt. 1, No. 9, May 15, 1944, p. 96, figs. 4-8.

Upper Pliocene (Rexroad fauna): Meade County, Kansas.

? Colinus eatoni SHUFELDT⁷¹

Colinus eatoni SHUFELDT, Trans. Connecticut Acad. Arts Sci., vol. 19, February 1915, p. 70, pl. 13, fig. 103.

Geologic age uncertain: Western Kansas.

⁷¹ Relationship uncertain. From the published figure it may possibly be an ocelline passeriform.

Genus **LOPHORTYX** Bonaparte

Lophortyx BONAPARTE, Geogr. and Comp. List, 1838, p. 42. Type, by subsequent designation, *Tetrao californicus* Shaw (Gray, 1840).

Lophortyx californicus (SHAW) : California Quail

Tetrao californicus SHAW, in Shaw and Nodder, Nat. Misc. vol. 9, 1798, text to pl. 345.

Modern form reported from late Pleistocene: Hawver Cave, Eldorado County, Carpinteria, McKittrick, Rancho La Brea, Los Angeles and San Pedro (Palos Verdes sand), Los Angeles County, California.

Genus **OREORTYX** Baird

Oreortyx BAIRD, Rep. Expl. and Surv. R. R. Pac., vol. 9, 1858, pp. xxi, xlv, 638, 642. Type, by original designation, *Ortyx picta* Douglas.

Oreortyx pictus (DOUGLAS) : Mountain Quail

Ortyx picta DOUGLAS, Trans. Linn. Soc. London, vol. 16, pt. 1, 1829, p. 143.

Modern form reported from late Pleistocene: Potter Creek and Samwel caves, Shasta County, and Hawver Cave, Eldorado County, California. Quaternary (probably Recent): Rocky Arroyo, New Mexico.

Genus **MIORTYX** Miller

Miortyx A. H. MILLER, Univ. California Publ., Bull. Dept. Geol. Sci., vol. 27, No. 4, June 22, 1944, p. 93. Type, by original designation, *Miortyx teres* Miller.

Miortyx teres MILLER

Miortyx teres A. H. MILLER, Univ. California Publ., Bull. Dept. Geol. Sci., vol. 27, No. 4, June 22, 1944, p. 93, fig. 7.

Lower Miocene (Rosebud formation): Flint Hill, 9 miles west-southwest of Martin, Bennett County, South Dakota.

Genus **CYRTONYX** Gould

Cyrtonyx GOULD, Monogr. Odontophoridae, pt. 1, 1844, pl. and text. Type, by monotypy, *Ortyx massena* Lesson = *Ortyx montezumae* Vigors.

Cyrtonyx montezumae (VIGORS) : Harlequin Quail

Ortyx Montezumae VIGORS, Zool. Journ., vol. 5, June 1830, p. 275.

Modern form reported from Pleistocene: San Josecito Cave, Aramberri, Nuevo León.

***Cyrtonyx cooki* WETMORE**

Cyrtonyx cooki WETMORE, Condor, vol. 36, No. 1, Jan. 15, 1934, p. 30, fig. 5.

Upper Miocene (Upper Sheep Creek beds): 17 miles south of Agate, Sioux County, Nebraska.

***Cyrtonyx tedfordi* MILLER⁷²**

Cyrtonyx tedfordi L. H. MILLER, Condor, vol. 54, No. 5, Sept. 22, 1952, p. 298, fig. 2.

Upper Miocene (Barstow formation): Lake bed horizon, near Barstow, California.

Subfamily PHASIANINAE: OLD WORLD PARTRIDGES and
PHEASANTS

Genus PHASIANUS Linnaeus

Phasianus LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 158. Type, by tautonymy, *Phasianus colchicus* Linnaeus.

***Phasianus alfhildae* SHUFELDT⁷³**

Phasianus alfhildae SHUFELDT, Trans. Connecticut Acad. Arts Sci., vol. 19, February 1915, p. 71.

Geologic age uncertain: 100 feet below horizon of Haystack Butte, Haystack Mountain, Wyoming.

Genus ARCHAEOPHASIANUS Lambrecht

Archaeophasianus LAMBRECHT, Handb. Palaeorn., 1933, p. 438. Type, by subsequent designation, *Phasianus roberti* Stone (Brodkorb, 1952).

***Archaeophasianus roberti* (STONE)**

Phasianus roberti STONE, Auk, vol. 32, No. 3, July (June 29), 1915, p. 376.

Lower Miocene (Middle John Day formation): Paulina⁷⁴ Creek, 6 miles from junction with Beaver Creek, Crook County, Oregon.

? *Archaeophasianus mioceanus* (SHUFELDT)⁷⁵

Phasianus mioceanus SHUFELDT, Trans. Connecticut Acad. Arts Sci., vol. 19, February 1915, p. 60, pl. 13, figs. 94, 96.

Miocene: Chimney Rock and Scott's Bluff, Nebraska.

⁷² Allocation in this genus tentative.

⁷³ Allocation of this species to the Old World genus *Phasianus* follows the usage of the original describer, and is subject to verification.

⁷⁴ Given as "Parilina" in the original place of publication, through an error in reading the field label.

⁷⁵ Described from fragmentary humerus and femur from the two separate localities listed. Probably a composite, with neither bone coming from a bird of this family. Assigned to *Archaeophasianus* by Lambrecht.

Family MELEAGRIDIDAE: TURKEYS

Genus MELEAGRIS Linnaeus

Meleagris LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 156. Type, by tautonymy, *Meleagris gallopavo* Linnaeus.

Meleagris gallopavo LINNAEUS: Turkey ⁷⁶

Meleagris Gallopavo LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 156.

Modern form reported from Upper Pliocene (Rexroad formation): Meade County Kansas. Pleistocene: Hartman's or Crystal Hill Cave, near Stroudsburg, and Durham Cave, near Riegelsville, Bucks County, and caves near Carlisle, Pennsylvania; North Liberty, St. Joseph County, Indiana; Ashmore, Coles County, Illinois; caves of Tennessee; fissure beds, Arkansas; Seminole Field, Pinellas County, Sarasota, Bradenton, Itchtucknee River, Melbourne, and cavern deposits at Ocala and Lecanto, Florida; near San Antonio, Socorro County, New Mexico.⁷⁷

Meleagris antiqua MARSH

Meleagris antiquus MARSH, Amer. Journ. Sci., ser. 3, vol. 2, August 1871, p. 126.

Oligocene (White River formation): "G Ranch," Colorado.

Meleagris celer MARSH

Meleagris celer MARSH, Amer. Journ. Sci., ser. 3, vol. 4, October 1872, p. 261.

Pleistocene: Monmouth County, New Jersey.

Meleagris richmondi SHUFELDT

Meleagris richmondi SHUFELDT, Trans. Connecticut Acad. Arts Sci., vol. 19, February 1915, p. 67, pl. 2, fig. 19.

Pleistocene: Near Mission San Jose, Alameda County, California.

Meleagris superba COPE

Meleagris superbus COPE, Trans. Amer. Philos. Soc., n.s., vol. 14, pt. 1, December 1870, p. 239.

Pleistocene: Monmouth County (type locality), and Manalapan,⁷⁸ New Jersey; Frankstown and Port Kennedy caves, Pennsylvania.

⁷⁶ *Ardea sellardsi* Shufeldt, 9th Ann. Rep. Florida State Geol. Surv., 1917, p. 38, pl. 2, fig. 15, from Vero (stratum 3) is a synonym of *Meleagris gallopavo* according to Wetmore, Smithsonian Misc. Coll., vol. 85, No. 2, Apr. 13, 1931, pp. 10-11, 32-33. The deposit is now considered to be of Recent age. See Cooke, Florida Geol. Surv. Geol. Bull. 29, 1945, pp. 306-307.

⁷⁷ Possibly Upper Pliocene.

⁷⁸ Type locality of *Meleagris altus* Marsh, Amer. Journ. Sci., ser. 3, vol. 4, 1872, p. 260, which is a synonym.

Meleagris tridens WETMORE

Meleagris tridens WETMORE, Smithsonian Misc. Coll., vol. 85, No. 2, Apr. 13, 1931, p. 33, fig. 13, pl. 6.

Pleistocene: Seminole Field, Pinellas County, Florida.

Meleagris crassipes MILLER

Meleagris crassipes L. H. MILLER, Condor, vol. 42, No. 3, May 15, 1940, p. 154, figs. 44-45.

Pleistocene: San Josecito Cave, Aramberri, Nuevo León.

Genus PARAPAVO Miller

Parapavo L. H. MILLER, Univ. California Publ., Bull. Dept. Geol., vol. 9, No. 9, Mar. 10, 1916, p. 96. Type, by monotypy, *Pavo californicus* Miller.

Parapavo californicus (MILLER)

Pavo californicus L. H. MILLER, Univ. California Publ., Bull. Dept. Geol., vol. 5, No. 19, Aug. 14, 1909, p. 285, pl. 25.

Upper Pliocene: Cita Canyon, Randall County, Texas. Pleistocene: York Valley site at Avenue 45 and Lincoln Avenue, Highland Park, Los Angeles, and southwest of La Habra near Los Angeles-Orange County line, California. Late Pleistocene: Carpinteria, and Rancho La Brea (type locality),⁷⁹ Los Angeles, California.

Order GRUIFORMES: CRANES, RAILS, and ALLIES**Suborder GRUES: CRANES, LIMPKINS, TRUMPETERS, and RAILS****Superfamily GRUOIDEA: CRANES, LIMPKINS, and TRUMPETERS****Family GERANOIDIDAE: GERANOIDES****Genus GERANOIDES** Wetmore

Geranoides WETMORE, Condor, vol. 35, No. 3, May 15, 1933, p. 115. Type, by original designation, *Geranoides jepseni* Wetmore.

Geranoides jepseni WETMORE

Geranoides jepseni WETMORE, Condor, vol. 35, No. 3, May 15, 1933, p. 115, fig. 22.

Lower Eocene (Gray Bull member): South Elk Creek, Bighorn County, Wyoming.

⁷⁹ Recorded also from early Recent deposits in Pit 10 at this site (Howard, H., and Miller, A. H., Carnegie Inst. Washington Publ. 514, 1939, p. 43). *Parapavo oklahomaensis* Stovall and Sandoz, Proc. Oklahoma Acad. Sci., vol. 16, 1936, p. 77, is a nomen nudum.

Family GRUIDAE: CRANES

Subfamily GRUINAE: CRANES

Genus ALETORNIS Marsh ⁸⁰

Aletornis MARSH, Amer. Journ. Sci., ser. 3, vol. 14, October 1872, p. 256.

Type, by subsequent designation, *Aletornis nobilis* Marsh (Hay, 1902).

***Aletornis bellus* MARSH ⁸¹**

Aletornis bellus MARSH, Amer. Journ. Sci., ser. 3, vol. 4, October 1872, p. 258.

Eocene (Bridger formation): Grizzly Buttes, Wyoming.

***Aletornis gracilis* MARSH ⁸¹**

Aletornis gracilis MARSH, Amer. Journ. Sci., ser. 3, vol. 4, October 1872, p. 258.

Eocene (Bridger formation): Henry's Fork, Wyoming.

***Aletornis nobilis* MARSH ⁸²**

Aletornis nobilis MARSH, Amer. Journ. Sci., ser. 3, vol. 4, October 1872, p. 256.

Eocene (Bridger formation): Grizzly Buttes, Wyoming.

***Aletornis pernix* MARSH**

Aletornis pernix MARSH, Amer. Journ. Sci., ser. 3, vol. 4, October 1872, p. 256.

Eocene (Bridger formation): Henry's Fork, Wyoming.

Genus FULICALETORNIS Lambrecht

Fulicaletornis LAMBRECHT, Handb. Palaeorn., 1933, p. 479. Type, by monotypy, *Aletornis venustus* Marsh.

⁸⁰ Allocation in the subfamily Gruinae provisional.

⁸¹ Considered by Shufeldt, Trans. Connecticut Acad. Arts Sci., vol. 19, February 1915, pp. 32, 76, as possibly a species of Scolopacidae.

⁸² Marsh in his original proposal of the genus *Aletornis* included in it five species without selecting a type. From the five in question Hay, U. S. Geol. Surv., Bull. 179, 1902, p. 527, designated *Aletornis nobilis* Marsh as genotype. Shufeldt, Trans. Connecticut Acad. Arts Sci., vol. 19, 1915, pp. 30, 31, placed *A. nobilis* in *Grus*, and described in the same paper (p. 77) *Grus marshi*. Lambrecht, Handb. Palaeorn., 1933, p. 520, proposed the genus *Protogrus* for *Aletornis nobilis* and *Grus marshi*, without designating a type. Lambrecht's action as regards *A. nobilis* obviously is erroneous as his proposed genus includes the genotype of *Aletornis*. *Aletornis nobilis*, therefore, is to be listed as above, and pending study *Grus marshi* is included tentatively under *Grus*. Brodkorb, Condor, vol. 54, No. 3, May 21, 1952, p. 175, has designated *A. nobilis*, already the type of *Aletornis* through action by Hay, as the type of *Protogrus*. That generic name therefore becomes a synonym of *Aletornis*.

Fulicaetornis venustus (MARSH)⁸³

Aletornis venustus MARSH, Amer. Journ. Sci., ser. 3, vol. 4, October 1872, p. 257.

Eocene (Bridger formation): Henry's Fork, Wyoming.

Genus PARAGRUS Lambrecht

Paragrus LAMBRECHT, Handb. Palacorn., 1933, p. 520. Type, by monotypy, *Gallinuloides prentici* Loomis.

Paragrus prentici (LOOMIS)

Gallinuloides prentici F. B. LOOMIS, Amer. Journ. Sci., ser. 4, vol. 22, December 1906, p. 481, figs. 1-3.

Eocene (Wasatch): Head of Elk Creek, 10 miles west of Otto, Wyoming.

Genus GRUS Pallas

Grus PALLAS, Misc. Zool., 1766, p. 66. Type, by tautonymy, *Ardea grus* Linnaeus.

Grus americana (LINNAEUS): Whooping Crane

Ardea americana LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 142.

Modern form reported from late Upper Pliocene: Snake River, 13 miles northwest of Grandview, Idaho. Pleistocene: Seminole Field, Pinellas County, Itchtucknee River, and Melbourne (stratum 2), Florida. Late Pleistocene: Rancho La Brea, Los Angeles, California.

Grus canadensis (LINNAEUS): Sandhill Crane⁸⁴

Ardea canadensis LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 141.

Modern form reported from Lower Pliocene (Upper Snake Creek beds): Sioux County, Nebraska. From ? Pleistocene: Niobrara River, Nebraska,⁸⁵ and Grizzly Buttes, Wyoming. From Pleistocene: Ash-

⁸³ Systematic allocation provisional. Shufeldt, Trans. Connecticut Acad. Arts Sci., vol. 19, February 1915, pp. 31, 32, 76, placed this species in the genus *Fulica*, the principal basis for Lambrecht's action in proposing *Fulicaetornis*.

⁸⁴ *Grus canadensis* is used as a species name to cover records of cranes of this type from the Pliocene and Pleistocene, including specimens that range in size from the modern little brown crane to the larger races of the sandhill crane.

Grus minor L. H. Miller, Univ. California Publ., Bull. Dept. Geol., vol. 5, August 1910, p. 446, fig. 8, from the Pleistocene of Rancho La Brea, is now considered by the describer as a synonym of *Grus canadensis*.

⁸⁵ This specimen, from either Pliocene or Pleistocene deposits, is the basis of *Grus haydeni* Marsh, Amer. Journ. Sci., ser. 2, vol. 49, 1870, p. 214, considered by Wetmore, Amer. Mus. Nov., No. 302, Feb. 29, 1928, p. 4, as a synonym of *Grus canadensis*.

more, Coles County, Illinois; Melbourne, Seminole Field, Pinellas County, and Bradenton, Florida. Late Pleistocene: Rancho La Brea, Los Angeles, and McKittrick, California.

***Grus proavus* MARSH**

Grus proavus MARSH, Amer. Journ. Sci., ser. 3, vol. 4, October 1872, p. 261.

Pleistocene: Monmouth County, New Jersey.

***Grus nannodes* WETMORE and MARTIN**

Grus nannodes WETMORE and MARTIN, Condor, vol. 32, No. 1, Jan. 20, 1930, p. 62, figs. 23-25.

Middle Pliocene (Ogallala formation, Edson beds): Sec. 25, T. 10 S., R. 38 W., Sherman County, Kansas.

***Grus conferta* MILLER and SIBLEY**

Grus conferta A. H. MILLER and C. G. SIBLEY, Condor, vol. 44, No. 3, May 15, 1942, p. 126, fig. 50.

Late Lower Pliocene (Siesta formation): Black Hawk Ranch, southern base of Mount Diablo, Contra Costa County, California.

***Grus marshi* SHUFELDT⁸⁶**

Grus marshi SHUFELDT, Trans. Connecticut Acad. Arts Sci., vol. 19, February 1915, p. 77, pl. 15, figs. 144-147.

Eocene (Bridger formation): Henry's Fork, Wyoming.

Family ARAMIDAE: LIMPKINS

Genus ARAMUS Vieillot

Aramus VIEILLOT, Analyse, 1816, p. 58. Type, by monotypy, *Courliri* Buffon = *Ardea scolopacea* Gmelin.

***Aramus guarauna* LINNAEUS: Limpkin**

Scolopax Guarauna LINNAEUS, Syst. Nat., ed. 12, vol. 1, 1766, p. 242.

Modern form reported from Pleistocene: Seminole Field, Pinellas County, and Itchtucknee River, Florida.

Genus BADISTORNIS Wetmore

Badistornis WETMORE, Journ. Morph., vol. 66, Jan. 2, 1940, p. 30. Type, by original designation, *Badistornis aramus* Wetmore.

⁸⁶ Generic allocation doubtful. See footnote under *Aletornis nobilis* (p. 59).

Badistornis aramus WETMORE

Badistornis aramus WETMORE, Journ. Morph., vol. 66, Jan. 2, 1940, p. 30, figs. 7-10.

Oligocene (*Metamynodon* zone, Brule formation): 35 miles southwest of Scenic, South Dakota.

Genus ARAMORNIS Wetmore

Aramornis WETMORE, Amer. Mus. Nov., No. 211, Mar. 11, 1926, p. 1. Type, by original designation, *Aramornis longurio* Wetmore.

Aramornis longurio WETMORE

Aramornis longurio WETMORE, Amer. Mus. Nov., No. 211, Mar. 11, 1926, p. 1, figs. 1-4.

Middle Miocene (Lower Sheep Creek beds): Snake Creek Quarries, Sioux County, Nebraska.

Genus GNOTORNIS Wetmore

Gnotornis WETMORE, Smithsonian Misc. Coll., vol. 101, No. 14, May 11, 1942, p. 1. Type, by monotypy, *Gnotornis aramiellus* Wetmore.

Gnotornis aramiellus WETMORE

Gnotornis aramiellus WETMORE, Smithsonian Misc. Coll., vol. 101, No. 14, May 11, 1942, p. 1, figs. 1-4.

Upper Oligocene (Upper Brule formation, *Protoceras-Leptauchenia* beds): 25 miles southeast of Scenic and 6 miles east of Rockyford, Washington County, South Dakota.

Superfamily RALLOIDEA: RAILS

Family RALLIDAE: RAILS, GALLINULES, and COOTS

Subfamily RALLINAE: RAILS

Genus TELMATORNIS Marsh ⁸⁷

Telmatornis MARSH, Amer. Journ. Sci., ser. 2, vol. 49, March 1870, p. 210. Type, by subsequent designation, *Telmatornis priscus* Marsh (Hay, 1902).

Telmatornis affinis MARSH

Telmatornis affinis MARSH, Amer. Journ. Sci., ser. 2, vol. 49, March 1870, p. 211.

Paleocene (Hornerstown marl): Hornerstown, New Jersey.

⁸⁷ Allocation in the subfamily Rallinae provisional.

Telmatornis priscus MARSH

Telmatornis priscus MARSH, Amer. Journ. Sci., ser. 2, vol. 49, March 1870, p. 210.

Paleocene (Hornerstown marl): Hornerstown, New Jersey.

Telmatornis rex SHUFELDT

Telmatornis rex SHUFELDT, Trans. Connecticut Acad. Arts Sci., vol. 19, February 1915, p. 27, pl. 13, fig. 101.

Paleocene (Hornerstown marl): Hornerstown, New Jersey.

Genus PALAEORALLUS Wetmore

Palacorallus WETMORE, Condor, vol. 33, No. 3, May 15, 1931, p. 108. Type, by original designation, *Palacorallus troxelli* Wetmore.

Palaeorallus troxelli WETMORE

Palacorallus troxelli WETMORE, Condor, vol. 33, No. 3, May 15, 1931, p. 108, figs. 26-29.

Lower Eocene (Wasatch formation): Northwest of Little Tatman Mountain, near Burlington, Wyoming.

Genus CRECCOIDES Shufeldt

Creccoides SHUFELDT, Proc. Amer. Philos. Soc., vol. 30, Apr. 14, 1892, p. 125. Type, by monotypy, *Creccoides osbornii* Shufeldt.

Creccoides osbornii SHUFELDT

Creccoides osbornii SHUFELDT, Proc. Amer. Philos. Soc., vol. 30, Apr. 14, 1892, p. 125.

Pliocene (Blanco fauna): Blanco Canyon, Crosby County, Texas.

Genus EPIRALLUS Miller

Epirallus L. H. MILLER, Univ. California Publ. Zoöl., vol. 47, Mar. 6, 1942, p. 43. Type, by monotypy, *Epirallus natator* Miller.

Epirallus natator MILLER

Epirallus natator L. H. MILLER, Univ. California Publ. Zoöl., vol. 43, Mar. 6, 1942, p. 43, fig. 1a.

Pleistocene: San Josecito Cave, Aramberri, Nuevo León.

Genus RALLUS Linnaeus

Rallus LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 153. Type, by subsequent designation, *Rallus aquaticus* Linnaeus (Fleming, 1821).

Rallus elegans AUDUBON: King Rail

Rallus elegans AUDUBON, Birds Amer. (folio), vol. 3, 1834, pl. 203.

Modern form reported from Pleistocene: Seminole Field, Pinellas County, and Itchtucknee River, Florida.

Rallus longirostris BODDAERT: Clapper Rail

Rallus longirostris BODDAERT, Table Planch. Enlum., 1783, p. 52.

Modern form reported from Pleistocene: Seminole Field, Pinellas County, Florida.

Rallus limicola VIEILLOT: Virginia Rail

Rallus limicola VIEILLOT, Nouv. Dict. Hist. Nat., nouv. éd., vol. 28, May 1819, p. 558.

Modern form recorded from Pleistocene: Reddick, Marion County, Florida. Late Pleistocene: Fossil Lake, Oregon; McKittrick, California.

Rallus prenticei WETMORE

Rallus prenticei WETMORE, Univ. Kansas Sci. Bull., vol. 30, pt. 1, No. 9, May 15, 1944, p. 99, figs. 9-19.

Upper Pliocene (Rexroad fauna): Meade County, Kansas.

Genus PORZANA Vieillot

Porzana VIEILLOT, Analyse, 1816, p. 61. Type, by monotypy and tautonymy, Marouette Buffon = *Rallus porzana* Linnaeus.

Porzana carolina (LINNAEUS): Sora

Rallus carolinus LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 153.

Pleistocene: Near Reddick, Marion County, Florida.

Porzana auffenbergi BRODKORB

Porzana auffenbergi BRODKORB, Condor, vol. 56, No. 2, Mar. 26, 1954, p. 103, fig. 1.

Pleistocene (stratum 2, shell layer, Sangamon stage): near Haile, Alachua County, Florida.

Genus LATERALLUS Gray

Laterallus G. R. GRAY, Cat. Gen. Subgen. Birds, 1855, p. 120. Type, by monotypy, *Rallus melanophaius* Vieillot.

Laterallus guti BRODKORB

Laterallus guti BRODKORB, Wilson Bull., vol. 64, No. 2, June 16, 1952, p. 80, fig. 1.

Pleistocene: 1 mile south of Reddick, Marion County, Florida.

Genus **ARAMIDES** Pucheran

Aramides PUCHERAN, Rev. Zool., vol. 8, August 1845, p. 277. Type, by original designation, *Fulica cayennensis* Gmelin.

Aramides cajanea (MÜLLER): **Wood Rail**

Fulica Cajanea P. L. S. MÜLLER, Natursyst. Suppl., 1776, p. 119.

Modern form reported from Pleistocene: Seminole Field, Pinellas County, Florida.

Genus **NESOTROCHIS** Wetmore

Nesotrochis WETMORE, Proc. U. S. Nat. Mus., vol. 54, Nov. 21, 1918, p. 516.
Type, by original designation, *Nesotrochis debooyi* Wetmore.

Nesotrochis debooyi WETMORE

Nesotrochis debooyi WETMORE, Proc. U. S. Nat. Mus., vol. 54, Nov. 21, 1918, p. 516, pl. 82.

Recent (extinct): ⁸⁸ Archeological sites on St. Thomas ⁸⁹ and St. Croix, Virgin Islands; and at Barrio Cañas, near Ponce; cavern deposits in Cueva Clara and Cueva San Miguel, near Morovis; Cueva Toraño, and a cave on Hacienda Jobo, near Utuado, Puerto Rico.

Subfamily **GALLINULINAE**: **GALLINULES**Genus **PORPHYRULA** Blyth

Porphyryla BLYTH, Cat. Birds Mus. Asiat. Soc., 1849 (1852), p. 283. Type, by monotypy, *P. chloronotus* Blyth = *Porphyrio alleni* Thomson.

Porphyryla martinica (LINNAEUS): **Purple Gallinule**

Fulica martinica LINNAEUS, Syst. Nat., ed. 12, vol. 1, 1766, p. 259.

Modern form reported from Pleistocene: Haile, Alachua County, Florida.

Genus **GALLINULA** Brisson

Gallinula BRISSON, Orn., 1760, vol. 1, p. 50; vol. 6, p. 2. Type, by tautonymy *Gallinula* Brisson = *Fulica chloropus* Linnaeus.

Gallinula chloropus (LINNAEUS): **Common Gallinule**

Fulica Chloropus LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 152.

Modern form reported from Upper Pliocene (Hagerman lake beds): Near Hagerman, Idaho. From Pleistocene: ⁹⁰ Seminole Field,

⁸⁸ Included here as it has not been found in living form, being known only from bones. Possibly the species lived until Spanish colonial times.

⁸⁹ Type locality a kitchen midden at Magen's Bay, on the north coast of St. Thomas.

⁹⁰ Reported from Pleistocene at Haile, Alachua County, Florida, on basis of a

Pinellas County, and Itchtucknee River, Florida. Late Pleistocene: Baños de Ciego Montero, Cuba.

Genus PALAEOCREX Wetmore⁹¹

Palaeocrex WETMORE, Proc. Colorado Mus. Nat. Hist., vol. 7, No. 2, July 15, 1927, p. 9. Type, by monotypy, *Palaeocrex fax* Wetmore.

Palaeocrex fax WETMORE

Palaeocrex fax WETMORE, Proc. Colorado Mus. Nat. Hist., vol. 7, No. 2, July 15, 1927, p. 9, figs. 15-18.

Lower Oligocene (Chadronian, Horsetail Creek facies): Horsetail Creek, Weld County, Colorado.

Genus EOCREX Wetmore

Eocrex WETMORE, Condor, vol. 33, No. 3, May 15, 1931, p. 107. Type, by original designation, *Eocrex primus* Wetmore.

Eocrex primus WETMORE

Eocrex primus WETMORE, Condor, vol. 33, No. 3, May 15, 1931, p. 107, figs. 21-25.

Lower Eocene ("Wasatch" formation): Near Steamboat Springs, Sweetwater County, Colorado (sec. 13, T. 24 N., R. 102 W., in Cathedral Bluffs).

Subfamily FULICINAE: Coots

Genus FULICA Linnaeus

Fulica LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 152. Type, by subsequent designation, *Fulica atra* Linnaeus (Gray, 1840).

Fulica americana GMELIN: American Coot

Fulica americana GMELIN, Syst. Nat., vol. 1, pt. 2, 1789, p. 704.

Modern form recorded from Upper Pliocene (Rexroad fauna): Meade County, Kansas. Pleistocene: Seminole Field, Pinellas County, Bradenton, Itchtucknee River, and Haile, Alachua County, Florida; Hemphill County, Texas; San Josecito Cave, Aramberri, Nuevo León. Late Pleistocene: Rancho La Brea, Los Angeles, and San Pedro (Palos Verdes formation), Los Angeles County, California.

cervical vertebra, by Brodkorb, Wilson Bull., vol. 65, No. 1, March (Apr. 22), 1953, p. 50.

⁹¹ Subfamily allocation provisional.

Fulica minor SHUFELDT⁹²

Fulica minor SHUFELDT, Amer. Nat., vol. 25, No. 297, September 1891, p. 820.

Late Pleistocene: Fossil Lake, Oregon.

Suborder CARIAMAE: CARIAMAS and ALLIES

Family BATHORNITHIDAE: BATHORNITHES

Genus **BATHORNIS** Wetmore

Bathornis WETMORE, Proc. Colorado Mus. Nat. Hist., vol. 7, No. 2, July 15, 1927, p. 11. Type, by monotypy, *Bathornis veredus* Wetmore.

Bathornis veredus WETMORE

Bathornis veredus WETMORE, Proc. Colorado Mus. Nat. Hist., vol. 7, No. 2, July 15, 1927, p. 11, figs. 19-24.

Lower Oligocene (Chadronian, Horsetail Creek facies): Horsetail Creek, Weld County, Colorado (type locality); near Crawford, Nebraska; Indian Creek, Pennington County, South Dakota.

Bathornis celeripes WETMORE

Bathornis celeripes WETMORE, Bull. Mus. Comp. Zoöl., vol. 75, October 1933, p. 302, figs. 6-14.

Upper Oligocene (Brule formation): Near Torrington, Goshen County, Wyoming (type locality); 12 miles northwest of Crawford, Nebraska.

Bathornis cursor WETMORE

Bathornis cursor WETMORE, Bull. Mus. Comp. Zoöl., vol. 75, October 1933, p. 310, figs. 15-19.

Upper Oligocene (Brule formation): Near Torrington, Goshen County, Wyoming.

Bathornis geographicus WETMORE

Bathornis geographicus WETMORE, Smithsonian Misc. Coll., vol. 101, No. 14, May 11, 1942, p. 3, figs. 5-13.

Upper Oligocene (Upper Brule formation, *Protoceras-Leptauchenia* beds): 25 miles southeast of Scenic and 6 miles east of Rockford, Washington County, South Dakota.

⁹² Howard (Carnegie Inst. Washington Publ. 551, Jan. 25, 1946, pp. 182-183) places all *Fulica* records from Fossil Lake, Oregon, under this name. She considers *minor* the Pleistocene ancestor of modern *Fulica americana*, listing it as *Fulica americana minor*, the relationship indicated by the trinomial expressing distribution through geologic time and not the geographic range of two sub-species existing simultaneously.

Order DIATRYMIFORMES: DIATRYMAS

Family DIATRYMIDAE: DIATRYMAS

Genus BARORNIS Marsh

Barornis MARSH, Amer. Journ. Sci., ser. 3, vol. 48, 1894, p. 344. Type, by monotypy, *Barornis regens* Marsh.

Barornis regens MARSH⁹³

Barornis regens MARSH, Amer. Journ. Sci., ser. 3, vol. 48, October 1894, p. 344, text fig.

Eocene: Squankum, Monmouth County, New Jersey.

Genus DIATRYMA Cope

Diatryma COPE, Proc. Acad. Nat. Sci. Philadelphia, vol. 28, sign. 2, April 18, 1876, p. 11. Type, by monotypy, *Diatryma gigantea* Cope.

Diatryma ajax SHUFELDT

Diatryma ajax SHUFELDT, Bull. Amer. Mus. Nat. Hist., vol. 32, art. 16, Aug. 4, 1913, p. 287, pl. 52, figs. 4-5, pl. 53, figs. 8-10, pl. 54, figs. 13-14.

Lower Eocene (Wasatch formation): 3 (type locality) and 5 miles southeast of mouth of Pat O'Hara Creek, Clark's Fork Basin, Wyoming.

Diatryma giganteum COPE

Diatryma gigantea COPE, Proc. Acad. Nat. Sci. Philadelphia, vol. 28, sign. 2, Apr. 18, 1876, p. 11.

Lower Eocene (Wasatch formation): New Mexico.⁹⁴

Diatryma steini MATTHEW and GRANGER

Diatryma steini MATTHEW and GRANGER, Bull. Amer. Mus. Nat. Hist., vol. 37, art. 11, May 28, 1917, p. 322, pls. 20-33.

Lower Eocene (Wasatch, Gray Bull member): South Elk Creek, Bighorn Basin, Wyoming.

Genus OMORHAMPHUS Sinclair

Omorhamphus SINCLAIR, Proc. Amer. Philos. Soc., vol. 67, 1928, p. 51. Type, by monotypy, *Omorhamphus storchii* Sinclair.

⁹³ Considered a species of *Diatryma* by Shufeldt, Trans. Connecticut Acad. Arts Sci., vol. 19, February 1915, pp. 37-38.

⁹⁴ Shufeldt, Trans. Connecticut Acad. Arts Sci., vol. 19, February 1915, p. 34, refers a fragment in Peabody Museum, Yale University, from Island Point, North Horseshoe, Gallina, New Mexico, to this species.

Omorhamphus storchii SINCLAIR

Omorhamphus storchii SINCLAIR, Proc. Amer. Philos. Soc., vol. 67, 1928, p. 52, pls. 1-2, figs. 1-3.

Lower Eocene (Lower Gray Bull horizon, Lower Wasatch): $1\frac{1}{2}$ miles southeast of Dorsey Creek, about 2 miles south of Otto-Basin Road, Big Horn County, Wyoming.

Order CHARADRIIFORMES: SHOREBIRDS, GULLS, and AUKS

Suborder CHARADRII: SHOREBIRDS

Superfamily CHARADRIOIDEA: PLOVERS, SANDPIPERS, and ALLIES

Family RHEGMINORNITHIDAE: RHEGMINORNIS

Genus RHEGMINORNIS Wetmore

Rhegminornis WETMORE, Proc. New England Zoöl. Club, vol. 22, June 23, 1943, p. 61. Type, by original designation, *Rhegminornis calobates* Wetmore.

Rhegminornis calobates WETMORE, Proc. New England Zoöl. Club, vol. 22, June 23, 1943, p. 61, pl. 11, figs. 1-5.

Lower Miocene (Tampa limestone): ⁹⁵ Thomas Farm, 8 miles north of Bell, Gilchrist County, Florida.

Family HAEMATOPODIDAE: OYSTERCATCHERS

Genus PARACTIORNIS Wetmore

Paractiornis WETMORE, Condor, vol. 32, No. 3, May 15, 1930, p. 133. Type, by monotypy, *Paractiornis perpusillus* Wetmore.

Paractiornis perpusillus WETMORE

Paractiornis perpusillus WETMORE, Condor, vol. 32, No. 3, May 15, 1930, p. 153, figs. 54-56.

Lower Miocene (Harrison formation): Carnegie Hill, Agate Fossil Quarry, near Agate, Sioux County, Nebraska.

⁹⁵ Cooke, Florida Geol. Surv., Geol. Bull. 29, 1945, pp. 119-120, believes that the specimen came from a sink in the Tampa limestone, rather than from the younger Hawthorn formation, to which it was ascribed by T. E. White, who collected it.

Genus **PALOSTRALEGUS** Brodkorb

Palostralegus BRODKORB, Florida Geol. Surv. Rep. Invest. No. 14, November 1955, p. 19. Type, by original designation, *Palostralegus sulcatus* Brodkorb.

Palostralegus sulcatus BRODKORB

Palostralegus sulcatus BRODKORB, Florida Geol. Surv. Rep. Invest. No. 14, November 1955, p. 20, fig. 18.

Pliocene (Bone Valley formation): Near Brewster, Polk County, Florida.

Family CHARADRIIDAE: PLOVERS, TURNSTONES, and SURFBIRDS

Subfamily CHARADRIINAE: PLOVERS

Genus **CHARADRIUS** Linnaeus

Charadrius LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 150. Type, by tautonymy, *Charadrius hiaticula* Linnaeus.

Charadrius sheppardianus COPE

Charadrius sheppardianus COPE, Bull. Geol. Geogr. Surv. Terr., vol. 6, No. 1, Feb. 11, 1881, p. 83.

Oligocene (Florissant lake beds): Florissant, Colorado.⁹⁰

Charadrius vociferus LINNAEUS: Killdeer

Charadrius vociferus LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 150.

Modern form reported from late Pleistocene: McKittrick, Kern County, and Rancho La Brea, Los Angeles, California.

Genus **EUPODA** Brandt

Eupoda J. F. BRANDT, in Tchihatchev, Voy. Sci. Altai Orient., 1845, p. 444. Type, by monotypy, *Charadrius asiaticus* Pallas.

Eupoda montana (TOWNSEND): Mountain Plover

Charadrius montanus J. K. TOWNSEND, Journ. Acad. Nat. Sci. Philadelphia, vol. 7, pt. 2, Nov. 21, 1837, p. 192.

Modern form reported from late Pleistocene: McKittrick, Kern County, California.

⁹⁰ Generic and subfamily allocation tentative, particularly since the Florissant beds now are held to be Oligocene rather than Miocene by most paleontologists.

Genus **SQUATAROLA** Cuvier

Squatarola CUVIER, Règne Animal, vol. 1, 1817 (Dec. 7, 1816), p. 467. Type, by tautonymy, *Tringa squatarola* Linnaeus.

Squatarola squatarola (LINNAEUS): Black-bellied Plover

Tringa Squatarola LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 149.

Modern form reported from late Pleistocene: Rancho La Brea, Los Angeles, California.

Genus **LIMICOLAVIS** Shufeldt ⁹⁷

Limicolavis SHUFELDT, Trans. Connecticut Acad. Arts Sci., vol. 19, February 1915, p. 55. Type, by monotypy, *Limicolavis pluvianella* Shufeldt.

Limicolavis pluvianella SHUFELDT

Limicolavis pluvianella SHUFELDT, Trans. Connecticut Acad. Arts Sci., vol. 19, February 1915, p. 55, pl. 15, fig. 129.

? Oligocene: Lower Willow Creek, Oregon.

Family SCOLOPACIDAE: WOODCOCK, SNIPES, and SANDPIPERS

Subfamily PALAEOTRINGINAE: PALAEOTRINGAS

Genus **PALAEOTRINGA** Marsh

Palaeotringa MARSH, Amer. Journ. Sci., ser. 2, vol. 49, March 1870, p. 208. Type, by subsequent designation, *Palaeotringa littoralis* Marsh (Hay, 1902).

Palaeotringa littoralis MARSH ⁹⁸

Palaeotringa littoralis MARSH, Amer. Journ. Sci., ser. 2, vol. 49, March 1870, p. 208.

Paleocene (Hornerstown marl): Hornerstown, New Jersey.

Palaeotringa vagans MARSH

Palaeotringa vagans MARSH, Amer. Journ. Sci., ser. 3, vol. 3, May 1872, p. 365.

Paleocene (Hornerstown marl): Hornerstown, New Jersey.

Palaeotringa vetus MARSH

Palaeotringa vetus MARSH, Amer. Journ. Sci., ser. 2, vol. 49, March 1870, p. 209.

Paleocene (Hornerstown marl): Arneytown, New Jersey.

⁹⁷ Family relationship uncertain.

⁹⁸ Shufeldt, Trans. Connecticut Acad. Arts Sci., vol. 19, February 1915, pp. 23, 77, pl. 6, fig. 35, believes this to be a gull, but this is open to question.

Subfamily SCOLOPACINAE: WOODCOCK and SNIPES

Genus CAPELLA Frenzel

Capella FRENZEL, Besch. Vögel und Eyer Wittenberg, 1801, p. 58. Type, by monotypy, *Scolopax coelestis* Frenzel = *Scolopax gallinago* Linnaeus.

Capella gallinago (LINNAEUS): Common Snipe⁹⁹

Scolopax Gallinago LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 147.

Modern form reported from late Pleistocene: Rancho La Brea, Los Angeles, California.

Capella anthonyi (WETMORE)

Gallinago anthonyi WETMORE, Proc. Biol. Soc. Washington, vol. 33, Dec. 30, 1920, p. 78, pl. 2, figs. 1, 2.

Recent (extinct):¹ Cave deposits in Cueva Catedral (type locality) and Cueva Clara, near Morovís, Puerto Rico.

Subfamily TRINGINAE: CURLEWS, YELLOWLEGS, and ALLIES

Genus NUMENIUS Brisson

Numenius BRISSON, Orn., 1760, vol. 1, p. 48; vol. 5, p. 311. Type, by tautonymy, *Numenius* Brisson = *Scolopax arquata* Linnaeus.

Numenius americanus BECHSTEIN: Long-billed Curlew

Numenius americanus BECHSTEIN, in Latham, Allgem. Uebers. Vögel, vol. 4, pt. 2, 1812, p. 432.

Modern form reported from late Pleistocene: McKittrick, Kern County, and Rancho La Brea, Los Angeles, California.

Numenius borealis (FORSTER): Eskimo Curlew

Scolopax borealis J. R. FORSTER, Philos. Trans., vol. 62, 1772, p. 431.

Modern form reported from late Pleistocene (Kentuck locality): McPherson County, Kansas.

Numenius phaeopus (LINNAEUS): Whimbrel²

Scolopax Phaeopus LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 146.

Modern form reported from late Pleistocene: Rancho La Brea, Los Angeles, California.

⁹⁹ *Capella delicata* (Ord), Wilson's snipe, of the previous list.

¹ Included here as it has not been found in living form, being known only from bones.

² *Phaeopus hudsonicus* (Latham), Hudsonian curlew of the previous list.

Genus **PALNUMENIUS** Miller

Palnumenius L. MILLER, Univ. California Publ. Zoöl., vol. 43, Mar. 6, 1942, p. 45. Type, by monotypy, *Palnumenius victima* Miller.

Palnumenius victima MILLER

Palnumenius victima L. MILLER, Univ. California Publ. Zoöl., vol. 43, Mar. 6, 1942, p. 45, fig. 1b.

Pleistocene: San Josecito Cave, Aramberri, Nuevo León.

Genus **BARTRAMIA** Lesson

Bartramia LESSON, Traité d'Orn., livr. 7, Apr. 9, 1831, p. 553. Type, by monotypy, *Bartramia laticauda* Lesson = *Tringa longicauda* Bechstein.

Bartramia longicauda (BECHSTEIN): Upland Plover

Tringa longicauda BECHSTEIN, in Latham, Allgem. Uebers. Vögel, vol. 4, pt. 2, 1812, p. 453.

Modern form reported from late Pleistocene: Meade County (Jones fauna, Vanhem formation), and McPherson County (Kentuck locality), Kansas.

Genus **TOTANUS** Bechstein

Totanus BECHSTEIN, Orn. Taschenb. Deutschland, vol. 2, 1803, p. 282. Type, by tautonymy, *Totanus maculatus* Bechstein = *Scolopax totanus* Linnaeus.

Totanus melanoleucus (GMELIN): Greater Yellowlegs

Scolopax melanoleuca GMELIN, Syst. Nat., vol. 1, pt. 2, 1789, p. 659.

Modern form reported from Pleistocene: Fossil Lake, Oregon; Rancho La Brea, Los Angeles, and McKittrick, Kern County, California.

Subfamily **CALIDRIINAE**: SANDPIPERS, GODWITS, and ALLIESGenus **CALIDRIS** Merrem

Calidris pacis MERREM, Lit. Zeitung, vol. 2, No. 168, June 8, 1804, col. 542. Type, by tautonymy, *Tringa calidris* Gmelin = *Tringa canutus* Linnaeus.

Calidris pacis BRODKORB

Calidris pacis BRODKORB, Florida Geol. Surv. Rep. Invest. No. 14, November 1955, p. 22, figs. 19, 20.

Pliocene (Bone Valley formation): Near Brewster, Polk County, Florida.

Genus *EROLIA* Vieillot

Erolia VIEILLOT, Analyse, 1816, p. 55. Type, by monotypy, *Erolia variegata* Vieillot = *Scolopax testacea* Pallas.

Erolia penepusilla BRODKORB

Erolia penepusilla BRODKORB, Florida Geol. Surv. Rep. Invest. No. 14, November 1955, p. 23, fig. 21.

Pliocene (Bone Valley formation): Near Brewster, Polk County, Florida.

Erolia alpina (LINNAEUS): Dunlin

Tringa alpina LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 149.

Modern form reported from late Pleistocene: McKittrick, Kern County, California.

Genus *LIMNODROMUS* Wied

Limnodromus WIED, Beitr. Naturg. Brasil, vol. 4, Abt. 2, 1833, p. 716. Type, by monotypy, *Scolopax noveboracensis* Gmelin = *Scolopax grisca* Gmelin.

Limnodromus griseus (GMELIN): Dowitcher

Scolopax grisca GMELIN, Syst. Nat., vol. 1, pt. 2, 1789, p. 658.

Modern form reported late Pleistocene: McKittrick, Kern County, and Rancho La Brea, Los Angeles, California.

Genus *MICROPALAMA* Baird

Micropalama BAIRD, Rep. Expl. and Surv. R. R. Pac., vol. 9, 1858, pp. xxii, xlvii, 714, 726. Type, by monotypy, *Tringa himantopus* Bonaparte.

Micropalama hesternus WETMORE

Micropalama hesternus WETMORE, Proc. U. S. Nat. Mus., vol. 64, art. 5, Jan. 15, 1924, p. 11, figs. 6-7.

Upper Pliocene (Blancan): 2 miles south of Benson, Arizona.

Genus *LIMOSA* Brisson

Limosa BRISSON, Orn., 1760, vol. 1, p. 48; vol. 5, p. 261. Type, by tautonymy, *Limosa* Brisson = *Scolopax limosa* Linnaeus.

Limosa vanrossemi MILLER

Limosa vanrossemi L. H. MILLER, Carnegie Inst. Washington Publ. 349, August 1925, p. 116, pl. 6.

Middle Miocene (Temblor, *Turritella ocoyana* zone): Lompoc, California.

Family RECURVIROSTRIDAE: IBIS-BILLS, AVOCETS, and STILTS

Subfamily RECURVIROSTRINAE: AVOCETS and STILTS

Genus RECURVIROSTRA Linnaeus

Recurvirostra LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 151. Type, by monotypy, *Recurvirostra avosetta* Linnaeus.

Recurvirostra americana GMELIN: Avocet

Recurvirostra americana GMELIN, Syst. Nat., vol. 1, pt. 2, 1789, p. 693.

Modern form reported from late Pleistocene: Fossil Lake, Oregon; Rancho La Brea, Los Angeles, and McKittrick, Kern County, California.

Genus HIMANTOPUS Brisson

Himantopus BRISSON, Orn., 1760, vol. 1, p. 46; vol. 5, p. 33. Type, by tautonymy, *Himantopus* Brisson = *Charadrius himantopus* Linnaeus.

Himantopus mexicanus (MÜLLER): Black-necked Stilt

Charadrius Mexicanus P. L. S. MÜLLER, Natursyst., Suppl., 1776, p. 117.

Modern form reported from late Pleistocene: Fossil Lake, Oregon.

Family PRESBYORNITHIDAE: PRESBYORNITHES

Genus PRESBYORNIS Wetmore

Presbyornis WETMORE, Ann. Carnegie Mus., vol. 16, Apr. 10, 1926, p. 396. Type, by monotypy, *Presbyornis pervetus* Wetmore.

Presbyornis pervetus WETMORE

Presbyornis pervetus WETMORE, Ann. Carnegie Mus., vol. 16, Apr. 10, 1926, p. 396, pl. 37, figs. 10-20.

Eocene (Lower Green River formation): White River, Utah, 2 miles from Colorado State line.

Family PHALAROPODIDAE: PHALAROPES

Genus LOBIPES Cuvier

Lobipes CUVIER, Règne Animal, vol. 1, 1817 (Dec. 7, 1816), p. 495. Type, by original designation, *Tringa hyperborea* Linnaeus = *Tringa lobata* Linnaeus.

Lobipes lobatus (LINNAEUS): Northern Phalarope

Tringa lobata LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 148.

Modern form reported from late Pleistocene: Fossil Lake, Oregon.

Suborder LARI: SKUAS, GULLS, TERNS, and SKIMMERS

Family STERCORARIIDAE: JAEGERs and SKUAS

Genus STERCORARIUS Brisson

Stercorarius BRISSON, Orn., 1760, vol. 1, p. 56; vol. 6, p. 149. Type, by tautonymy, *Stercorarius* Brisson = *Larus parasiticus* Linnaeus.

Stercorarius shufeldti HOWARD

Stercorarius shufeldti H. HOWARD, Carnegie Inst. Washington Publ. 551, Jan. 25, 1946, p. 184, pl. 2, figs. 1, 2.

Late Pleistocene: Fossil Lake, Oregon.³

Family LARIDAE: GULLS and TERNS

Subfamily LARINAE: GULLS

Genus LARUS Linnaeus⁴

Larus LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 136. Type, by subsequent designation, *Larus marinus* Linnaeus (Selby, 1840).

Larus glaucescens NAUMANN: Glaucous-winged Gull

Larus glaucescens NAUMANN, Naturg. Vogel Deutschl., vol. 10, 1840, p. 351.

Modern form reported from late Pleistocene (Palos Verdes formation): San Pedro, Los Angeles County, California.

Larus californicus LAWRENCE: California Gull

Larus Californicus LAWRENCE, Ann. Lyc. Nat. Hist. New York, vol. 6, 1854, p. 79.

Modern form reported from late Pleistocene: Fossil Lake, Oregon.

Larus philadelphia (ORD): Bonaparte's Gull

Sterna Philadelphia ORD, in Guthrie, Geogr., 2d Amer. ed., 1815, p. 319.

Modern form reported from late Pleistocene: Fossil Lake, Oregon.⁵

Larus oregonus SHUFELDT

Larus oregonus SHUFELDT, Amer. Nat., vol. 25, No. 297, September 1891, p. 820.

Late Pleistocene: Fossil Lake, Oregon.

³ The type of *Stercorarius shufeldti* originally was identified by Shufeldt as *Larus argentatus*, this specimen being the basis for the record of the herring gull from Fossil Lake.

⁴ *Larus vero* Shufeldt, Journ. Geol., January-February 1917, p. 18, has been identified by Wetmore as *Nyctanassa violacea* Linnaeus (Smithsonian Misc. Coll., vol. 85, No. 2, Apr. 13, 1931, p. 16).

⁵ Records of *Xema sabini* from Fossil Lake, so far as identified, refer to *Larus philadelphia*.

Larus pristinus SHUFELDT⁶

Larus pristinus SHUFELDT, Trans. Connecticut Acad. Arts Sci., vol. 19, February 1915, p. 54, pl. 14, fig. 112.

? Oligocene (John Day) : Willow Creek, Oregon.

Larus robustus SHUFELDT

Larus robustus SHUFELDT, Amer. Nat., vol. 25, No. 297, September 1891, p. 819.

Late Pleistocene : Fossil Lake, Oregon.

Larus elmorei BRODKORB

Larus elmorei BRODKORB, Wilson Bull., vol. 65, No. 2, June 30, 1953, p. 94, fig. 1.

Pliocene (Bone Valley formation) : Near Brewster, Polk County, Florida.

Genus GAVIOTA Miller and Sibley⁷

Gaviota A. H. MILLER and C. G. SIBLEY, Auk, vol. 58, No. 4, October 1941, p. 563. Type, by monotypy, *Gaviota niobrara* Miller and Sibley.

Gaviota niobrara MILLER and SIBLEY

Gaviota niobrara A. H. MILLER and C. G. SIBLEY, Auk, vol. 58, No. 4, October 1941, p. 563, fig. 1.

Late Upper Miocene (Barstovian, Niobrara River zone) : Niobrara Game Preserve, Cherry County, Nebraska.

Subfamily STERNINAE : TERNS**Genus STERNA** Linnaeus

Sterna LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 137. Type, by tautonymy, *Sterna hirundo* Linnaeus.

Subgenus STERNA Linnaeus**Sterna forsteri** NUTTALL : Forster's Tern

Sterna forsteri NUTTALL, Manual Orn. U. S. and Canada, vol. 2, 1834, p. 274.

Modern form reported from late Pleistocene : Fossil Lake, Oregon.

Genus CHLIDONIAS Rafinesque

Chlidonias RAFINESQUE, Kentucky Gazette, n. s., vol. 1, No. 8, Feb. 21, 1822, p. 3, col. 5. Type, by monotypy, *Sterna melanops* Rafinesque = *Sterna surinamensis* Gmelin.

⁶ Generic assignation in original description tentative.

⁷ Allocation to subfamily provisional.

Chlidonias niger (LINNAEUS) : Black Tern

Sterna nigra LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 137.

Modern form reported from late Pleistocene: Fossil Lake, Oregon,

Suborder ALCAE: AUKS

Family ALCIDAE: AUKS, MURRES, and PUFFINS

Subfamily NAUTILORNITHINAE: NAUTILORNITHES

Genus NAUTILORNIS Wetmore

Nautilornis WETMORE, Ann. Carnegie Mus., vol. 16, Apr. 10, 1926, p. 392.
Type, by original designation, *Nautilornis avus* Wetmore.

Nautilornis avus WETMORE

Nautilornis avus WETMORE, Ann. Carnegie Mus., vol. 16, Apr. 10, 1926, p. 392,
pl. 36, figs. 1-8.

Eocene (Lower Green River formation): White River, Utah, 2 miles from Colorado State line.

Nautilornis proavitus WETMORE

Nautilornis proavitus WETMORE, Ann. Carnegie Mus., vol. 16, Apr. 10, 1926,
p. 394, pl. 36, fig. 9.

Eocene (Lower Green River formation): White River, Utah, 2 miles from Colorado State line.

Genus HYDROTHERIKORNIS Miller

Hydrotherikornis A. H. MILLER, Univ. California Publ., Bull. Dept. Geol. Sci.,
vol. 20, No. 3, Apr. 21, 1931, p. 24. Type, by monotypy, *Hydrotherikornis oregonus* Miller.

Hydrotherikornis oregonus MILLER

Hydrotherikornis oregonus A. H. MILLER, Univ. California Publ., Bull. Dept.
Geol. Sci., vol. 20, No. 3, Apr. 21, 1931, p. 24, fig. 1.

Upper Eocene (Arago series): Sunset Bay, near Coos Bay, Coos County, Oregon.

Subfamily ALCINAE: AUKS and MURRES

Genus AUSTRALCA Brodkorb

Australca BRODKORB, Florida Geol. Surv. Rep. Invest. No. 14, November 1955,
p. 25. Type, by original designation, *Australca grandis* Brodkorb.

***Australca grandis* BRODKORB**

Australca grandis BRODKORB, Florida Geol. Surv. Rep. Invest. No. 14, November 1955, p. 27, figs. 24, 29.

Pliocene (Bone Valley formation): Near Brewster, Polk County, Florida.

Genus *URIA* Brisson

Uria BRISSON, Orn., 1760, vol. 1, p. 52; vol. 6, p. 70. Type, by tautonymy, *Uria* Brisson = *Colymbus aalge* Pontoppidan.

***Uria aalge* (PONTOPPIDAN): Common Murre**

Colymbus aalge PONTOPPIDAN, Danske Atlas, vol. 1, 1763, p. 621, pl. 26.

Modern form reported from late Pleistocene (Palos Verdes sand): Playa del Rey, and Mussel Rock, San Mateo County, California.

***Uria affinis* (MARSH)**

Catarractes affinis MARSH, Amer. Journ. Sci., ser. 3, vol. 4, October 1872, p. 259.

Pleistocene: Railroad cut on bank of Penobscot River, near Bangor, Maine.

***Uria antiqua* (MARSH)**

Catarractes antiquus MARSH, Amer. Journ. Sci., ser. 2, vol. 49, March 1870, p. 213.

Miocene: Tarboro, Edgecombe County, North Carolina.

Genus *MIOCEPPHUS* Wetmore

Miocepphus WETMORE, Journ. Morph., vol. 66, Jan. 2, 1940, p. 35. Type, by monotypy, *Miocepphus mcclungi* Wetmore.

***Miocepphus mcclungi* WETMORE**

Miocepphus mcclungi WETMORE, Journ. Morph., vol. 66, Jan. 2, 1940, p. 35, figs. 11-14.

Miocene (Calvert formation, zone 12): Near the mouth of Parker Creek, Calvert County, Maryland.⁸

Genus *BRACHYRAMPHUS* Brandt

Brachyramphus M. BRANDT, Bull. Sci. Acad. Imp. Sci. St.-Petersbourg, vol. 2, No. 22, Mar. 19, 1837, col. 346. Type, by subsequent designation, *Colymbus marmoratus* Gmelin (Gray, 1840).

⁸ Two records.

Brachyramphus pliocenium HOWARD

Brachyramphus pliocenium HOWARD, Carnegie Inst. Washington Publ. 584, June 22, 1949, p. 191.

Middle Pliocene (San Diego formation): Washington Boulevard Freeway, San Diego, California.

Genus SYNTHLIBORAMPHUS Brandt

Synthliboramphus M. BRANDT, Bull. Sci. Acad. Imp. Sci. St.-Petersbourg, vol. 2, No. 22, Mar. 19, 1837, col. 347. Type, by subsequent designation, *Alca antiqua* Gmelin (Gray, 1840).

Synthliboramphus antiquum (Gmelin): Ancient Murrelet

Alca antiqua Gmelin, Syst. Nat., vol. 1, pt. 2, 1789, p. 554.

Modern form reported from late Pleistocene (Palos Verdes sand): San Pedro, California.

Genus PTYCHORAMPHUS Brandt

Ptychoramphus M. BRANDT, Bull. Sci. Acad. Imp. Sci. St.-Petersbourg, vol. 2, No. 22, Mar. 19, 1837, col. 347. Type, by monotypy, *Uria aleutica* Pallas.

Ptychoramphus aleuticum (Pallas): Cassin's Auklet

Uria Aleutica PALLAS, Zoogr. Rosso-Asiatica, vol. 2, 1811, p. 370.

Modern form reported from late Pleistocene (Palos Verdes sand): San Pedro, Los Angeles County, California.

Genus CERORHINCA Bonaparte

Cerorhinca BONAPARTE, Ann. Lyc. Nat. Hist. New York, vol. 2, 1828, p. 427. Type, by monotypy, *Cerorhinca occidentalis* Bonaparte = *Alca monocerata* Pallas.

Cerorhinca dubia MILLER

Cerorhinca dubia L. H. MILLER, Carnegie Inst. Washington Publ. 349, August 1925, p. 115, pl. 2.

Middle Miocene (Temblor, *Turritella ocoyana* zone): Lompoc, California.

Family MANCALLIDAE: LUCAS AUK and ALLY**Genus MANCALLA** Lucas

Mancalla LUCAS, Science, n.s., vol. 13, Mar. 15, 1901, p. 428. Type, by original designation, *Mancalla californiensis* Lucas.

Mancalla californiensis LUCAS

Mancalla californiensis LUCAS, Science, n.s., vol. 13, Mar. 15, 1901, p. 428.⁹

Pliocene: Third Street Tunnel, Los Angeles (type locality), and Newport Bay. Middle Pliocene (San Diego formation): San Diego, San Diego County, and Corona del Mar, Orange County, California.

Mancalla diegensis (MILLER)

Pliolunda diegensis L. H. MILLER, Trans. San Diego Soc. Nat. Hist., vol. 8, Dec. 15, 1937, p. 376, 2 figs.

Middle Pliocene (San Diego formation): Market Street, near Euclid Avenue (type locality), and Mission Hills district, San Diego, California.

Order COLUMBIFORMES: SAND-GROUSE, PIGEONS, AND DOVES

Suborder COLUMBAE: PIGEONS and DOVES

Family COLUMBIDAE: PIGEONS and DOVES

Subfamily COLUMBINAE: PIGEONS and DOVES

Genus COLUMBA Linnaeus

Columba LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 162. Type, by subsequent designation, *Columba oenas* Linnaeus (Vigors, 1825).

Columba fasciata SAY: Band-tailed Pigeon

Columba fasciata SAY, in Long, Exped. Rocky Mountains, vol. 2, 1823, p. 10.

Modern form reported from late Pleistocene: Stone Man Cave, Shasta County, Rancho La Brea, Los Angeles, and Carpinteria, Santa Barbara County, California. Pleistocene: San Josecito Cave, Aramberri, Nuevo León.

Columba micula (WETMORE)

Chloranas micula WETMORE, Proc. U. S. Nat. Mus., vol. 64, art. 5, Jan. 15, 1924, p. 13, figs. 8-9.

Early Pleistocene: Curtis Ranch, 12 miles southeast of Benson, Arizona.

Genus ZENAIDURA Bonaparte

Zenaidura BONAPARTE, Compt. Rend. Acad. Sci. Paris, vol. 40, January 1855, p. 96. Type, by original designation, *Columba carolinensis* Linnaeus.

⁹ See also Lucas, Proc. U. S. Nat. Mus., vol. 24, Sept. 27, 1901, pp. 133-134, figs. 1, 2.

Zenaidura macroura (LINNAEUS): Mourning Dove

Columba macroura LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 164.

Modern form reported from Upper Pliocene (Rexroad fauna): Meade County, Kansas. Pleistocene: San Josecito Cave, Aramberri, Nuevo León; Seminole Field, Pinellas County, Florida. Late Pleistocene: Carpinteria, Santa Barbara County, McKittrick, Kern County, and Rancho La Brea, Los Angeles, California; Meade County, Kansas (Vanhem formation, Jones fauna).

Genus ECTOPISTES Swainson

Ectopistes SWAINSON, Zool. Journ., vol. 3, No. 11, September-December 1827, p. 362. Type, by subsequent designation, *Columba migratoria* Linnaeus (Swainson, 1837).

Ectopistes migratorius (LINNAEUS): Passenger Pigeon

Columba migratoria LINNAEUS, Syst. Nat., ed. 12, vol. 1, 1766, p. 285.

Modern form reported from Pleistocene: Cave deposits of Tennessee. Late Pleistocene: Rancho La Brea, Los Angeles, California.

Genus GEOTRYGON Gosse

Geotrygon GOSSE, Birds Jamaica, 1847, p. 316. Type, by subsequent designation, *Columba cristata* Latham = *Geotrygon sylvatica* Gosse = *Columbigallina versicolor* Lafresnaye (Reichenbach, 1852 = 1853).

Geotrygon larva (WETMORE)

Orcopelcia larva WETMORE, Proc. Biol. Soc. Washington, vol. 33, Dec. 30, 1920, p. 79, pl. 3, figs. 1-2.

Recent (extinct):¹⁰ Cave deposits in Cueva Clara (type locality) and Cueva Catedral, near Morovís; Cueva Toraño, near Utuado; kitchen middens near Mayagüez, and at Barrio Cañas, near Ponce, Puerto Rico.

Order PSITTACIFORMES: LORIES, PARROTS, PARAKEETS, and MACAWS

Family PSITTACIDAE: LORIES, PARROTS, and MACAWS

Subfamily PSITTACINAE: PARAKEETS and MACAWS

Genus ARA Lacépède

Ara LACÉPÈDE, Tableaux Ois., 1799, p. 1, Type, by subsequent designation, *Psittacus macao* Linnaeus (Ridgway, 1916).

¹⁰ Included here as it has not been found in living form, being known only from bones.

Ara tricolor BECHSTEIN: **Cuban Macaw**

Ara tricolor BECHSTEIN, in Latham, Allg. Uebers. Vög., vol. 4, Th. 1, 1811, p. 64, pl. 1. (Cuba.)

Modern form recorded from late Pleistocene: Baños de Ciego Montero, Santa Clara Province, Cuba.

Ara autocthonos WETMORE

Ara autocthonos WETMORE, Journ. Agr. Univ. Puerto Rico, vol. 21, No. 1, January 1937, p. 12, pl. 1, figs. 8, 9.

Recent (extinct):¹¹ Prehistoric kitchen midden deposits at Concordia, near Southwest Cape, St. Croix, Virgin Islands.

Genus RHYNCHOPSITTA Bonaparte

Rhynchopsitta BONAPARTE, Rev. et Mag. Zool., ser. 2, vol. 6, March 1854, p. 149. Type, by monotypy, *Macrocerus pachyrhynchus* Swainson.

Rhynchopsitta pachyrhyncha (SWAINSON): **Thick-billed Parrot**

Macrocerus pachyrhynchus SWAINSON, Philos. Mag., n.s., vol. 1, No. 6, June 1827, p. 439.

Modern form reported from Pleistocene: San Josecito Cave, Aramberri, Nuevo León.

Genus CONUROPSIS Salvadori

Conuropsis SALVADORI, Cat. Birds Brit. Mus., vol. 20, 1891, pp. 146, 203. Type, by original designation, *Psittacus carolinensis* Linnaeus.

Conuropsis fratercula WETMORE

Conuropsis fratercula WETMORE, Amer. Mus. Nov., No. 211, Mar. 11, 1926, p. 3, figs. 5-6.

Middle Miocene (*Merychippus primus* zone, lower Sheep Creek beds): Snake Creek Quarries, Sioux County, Nebraska.

Order CUCULIFORMES: PLANTAIN-EATERS and CUCKOOS

Suborder CUCULI: CUCKOOS, ROADRUNNERS, and ANIS

Family CUCULIDAE: CUCKOOS, ROADRUNNERS, and ANIS

Subfamily NEOMORPHINAE: GROUND CUCKOOS

Genus GEOCOCCYX Wagler

Geococcyx WAGLER, Isis von Oken, vol. 24, Heft 5, May 1831, col. 524. Type, by monotypy, *Geococcyx variegata* Wagler = *Saurothera californiana* Lesson.

¹¹ Included here since it has not been found in living form, being known only from bones.

Geococcyx californianus (LESSON) : Roadrunner

Saurothera californiana LESSON, Compl. Oeuvres Buffon, vol. 6, 1829, p. 420.

Modern form reported from late Pleistocene: Rancho La Brea, Los Angeles, McKittrick, Kern County, and Carpinteria, Santa Barbara County, California.

Geococcyx conklingi HOWARD

Geococcyx conklingi HOWARD, Condor, vol. 33, No. 5, Sept. 15, 1931, p. 208, figs. 49-50.

Pleistocene: Conkling Cavern (type locality), and Shelter Cave,¹² Pyramid Peak, Organ Mountains, Dona Ana County, New Mexico; San Josecito Cave, Aramberri, Nuevo León.

Order STRIGIFORMES: OWLS¹³**Family PROTOSTRIGIDAE: PROTOSTRIX****Genus PROTOSTRIX Wetmore**

Protostrix WETMORE, Amer. Mus. Nov., No. 680, Dec. 4, 1933, p. 3. Type, by original designation, *Aquila lydekkeri* Shufeldt.

Protostrix lydekkeri (SHUFELDT)

Aquila lydekkeri SHUFELDT, Bull. Amer. Mus. Nat. Hist., vol. 32, art. 16, Aug. 4, 1913, p. 298.

Eocene (Bridger formation) : Lower Cottonwood Creek, Wyoming.

Protostrix saurodosis (WETMORE)

Mincerua saurodosis WETMORE, Proc. Acad. Nat. Sci. Philadelphia, vol. 73, 1921 (Apr. 6, 1922), p. 455, figs. 1-2.

Eocene (Bridger formation) : Near Lodgepole Trail Crossing on Dry Creek, about 10 miles from Fort Bridger, Wyoming.

Protostrix leptosteus (MARSII)¹⁴

Bubo leptosteus MARSII, Amer. Journ. Sci., ser. 3, vol. 2, August 1871, p. 126.

Eocene (Bridger formation) : Grizzly Buttes, near Fort Bridger, Wyoming.

¹² Possibly of Recent period.

¹³ *Aquila ontigua* Shufeldt, type of the genus *Mincerua* Shufeldt, formerly considered an owl, proves to be a mammal. See Wetmore, Amer. Mus. Nov., No. 680, Dec. 4, 1933, pp. 1, 2.

¹⁴ See Wetmore, Condor, 1937, pp. 84-85.

Protostrix mimica WETMORE

Protostrix mimica WETMORE, Proc. U. S. Nat. Mus., vol. 85, Jan. 17, 1938, p. 27, figs. 4-5

Lower Eocene (Wasatch): South side of Ten Mile Creek, 12 miles northwest of Worland, Wyoming.

Family TYTONIDAE: BARN OWLS

Subfamily TYTONINAE: BARN OWLS

Genus **TYTO** Billberg

Tyto BILLBERG, Syn. Faunae Scand., vol. 1, pt. 2, 1828, tab. A. Type, by monotypy, *Strix flammea* auct. = *Strix alba* Scopoli.

Tyto alba (SCOPOLI): Barn Owl

Strix alba SCOPOLI, Annus 1, Historico-Naturalis, 1769, p. 21.

Modern form reported from Pleistocene: Cavern deposits near Lecanto, Florida;¹⁵ San Josecito Cave, Aramberri, Nuevo León. Late Pleistocene: Carpinteria, Santa Barbara County and Rancho La Brea, Los Angeles, California.

Tyto cavatica WETMORE

Tyto cavatica WETMORE, Proc. Biol. Soc. Washington, vol. 33, Dec. 30, 1920, p. 80, pl. 3, figs. 3-6.

Recent (extinct):¹⁶ Cave deposits in Cueva Toraño, near Utuado, Puerto Rico.

Tyto ostologa WETMORE

Tyto ostologa WETMORE, Smithsonian Misc. Coll., vol. 74, No. 4, Oct. 17, 1922, p. 2.

Recent (extinct):¹⁶ Cave deposits in Grotte San Francisco near St. Michel (type locality), and caves near L'Atalye, Haiti.

Tyto pollens WETMORE

Tyto pollens WETMORE, Bull. Mus. Comp. Zoöl., vol. 80, No. 12, October 1937, p. 436, figs. 10-16.

Recent (extinct):¹⁶ Cave deposits on Great Exuma Island, Bahama Islands.

¹⁵ The record from Vero (stratum 3) is now considered to be of Recent age. See Cooke, Florida Geol. Surv., Geol. Bull. 29, 1945, pp. 306-307.

¹⁶ Included here as it has not been found in living form, being known only from bones.

Family STRIGIDAE: TYPICAL OWLS

Genus OTUS Pennant

Otus PENNANT, Indian Zool., 1769, p. 3. Type, by monotypy, *Otus bakkamoena* Pennant.

Otus asio (LINNAEUS): Screech Owl

Strix asio LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 92.

Modern form reported from Pleistocene: Cavern deposits near Lecanto, Florida; cave deposits of Tennessee; San Josecito Cave, Aramberri, Nuevo León. Late Pleistocene: Potter Creek Cave, Shasta County, Carpinteria, Santa Barbara County, and Rancho La Brea, Los Angeles, California.

Otus flammeolus (KAUP): Flammulated Owl

Scops (Megascops) flammeola KAUP, in Jardine, Contr. Orn., 1852 (1853), p. 111.

Modern form reported from Pleistocene: San Josecito Cave, Aramberri, Nuevo León. Late Pleistocene: Samwel Cave,¹⁷ Shasta County, California.

Otus trichopsis (WAGLER): Whiskered Owl

Scops trichopsis WAGLER, Isis von Oken, Heft 3, March 1832, col. 276.

Modern form reported from Pleistocene: San Josecito Cave, Aramberri, Nuevo León.

Genus BUBO Duméril

Bubo DUMÉRIL, Zool. Analytique, 1806, p. 34. Type, by tautonymy, *Strix bubo* Linnaeus.

Bubo virginianus (GMELIN): Horned Owl

Strix virginiana GMELIN, Syst. Nat., vol. 1, pt. 1, 1788, p. 287.

Modern form reported from late Pleistocene: Fossil Lake, Oregon; Samwel Cave, Shasta County, Carpinteria, Santa Barbara County, McKittrick, Kern County, and Rancho La Brea, Los Angeles, California. Pleistocene: San Josecito Cave, Aramberri, Nuevo León.

Bubo sinclairi MILLER

Bubo sinclairi L. H. MILLER, Univ. California Publ., Bull. Dept. Geol., vol. 6, No. 16, Oct. 28, 1911, p. 393, figs. 4-5.

Late Pleistocene: Samwel and Potter Creek (type locality) caves, Shasta County, California.

¹⁷ Recorded originally as *Micropallas whitneyi*. See Miller, L. H., Trans. San Diego Soc. Nat. Hist., vol. 7, No. 19, Mar. 31, 1933, pp. 209-210.

Genus GLAUCIDIUM Boie

Glaucidium BOIE, Isis von Oken, Bd. 2, 1826, col. 970. Type, by subsequent designation, *Strix passerina* Linnaeus (Gray, 1840).

***Glaucidium gnoma* WAGLER: Pygmy Owl**

Glaucidium Gnoma WAGLER, Isis von Oken, vol. 25, Heft 3, March 1832, p. 275.

Modern form reported from late Pleistocene: Samwel Cave, Shasta County, Carpinteria, Santa Barbara County, and Rancho La Brea, Los Angeles, California.

Genus SPEOTYTO Gloger

Speotyto GLOGER, Hand- und Hilfsbuch Naturg., 1842 (1841), p. 226. Type, by monotypy, *Strix cunicularia* Molina.

***Speotyto cunicularia* (MOLINA): Burrowing Owl**

Strix Cunicularia MOLINA, Sagg. Stor. Nat. Chili, 1782, p. 263.

Modern form reported from late Pleistocene: McKittrick, Kern County, and Rancho La Brea, Los Angeles, California.

Genus CICCABA Wagler

Ciccaba WAGLER, Isis von Oken, Heft 11, 1832, col. 1222. Type, by monotypy, *Ciccaba huhula* = *Strix huhula* Daudin.

***Ciccaba virgata* (CASSIN): Mottled Owl**

Syrnium virgatum CASSIN, Proc. Acad. Nat. Sci. Philadelphia, vol. 4, 1848 (1850), p. 124.

Modern form reported from Pleistocene: San Josecito Cave, Aramberri, Nuevo León.

Genus STRIX Linnaeus

Strix LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 92. Type, by tautonymy, *Strix stridula* Linnaeus = *Strix aluco* Linnaeus.

***Strix varia* BARTON: Barred Owl**

Strix varius BARTON, Fragm. Nat. Hist. Pennsylvania, 1799, p. 11.

Modern form reported from Pleistocene: Seminole Field, Pinellas County, Melbourne, and cavern deposits near Lecanto, Florida.

***Strix occidentalis* (XANTUS): Spotted Owl**

Syrnium occidentale XANTUS, Proc. Acad. Nat. Sci. Philadelphia, 1859 (Jan. 10, 1860), p. 193.

Modern form reported from Pleistocene: San Josecito Cave, Aramberri, Nuevo León.

Strix brea HOWARD

Strix brea HOWARD, Condor, vol. 35, No. 2, Mar. 15, 1933, p. 66, fig. 15.

Late Pleistocene: Rancho La Brea, Los Angeles, California.

Strix dakota MILLER

Strix dakota A. H. MILLER, Univ. California Publ., Bull. Dept. Geol. Sci., vol. 27, No. 4, June 22, 1944, p. 95, fig. 8.

Lower Miocene (Rosebud formation): Flint Hill, 9 miles west-southwest of Martin, Bennett County, South Dakota.

Genus ASIO Brisson

Asio BRISSON, Orn., 1760, vol. 1, p. 28. Type, by tautonymy, *Asio* Brisson = *Strix otus* Linnaeus.

Asio otus (LINNAEUS):¹⁸ Long-eared Owl

Strix Otus LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 92.

Modern form reported from late Pleistocene: Samwel Cave, Shasta County, McKittrick, Kern County, and Carpinteria, Santa Barbara County, California.¹⁹ Pleistocene: San Josecito Cave, Aramberri, Nuevo León.

Asio flammeus (PONTOPPIDAN): Short-eared Owl

Strix flammea PONTOPPIDAN, Danske Atlas, vol. 1, 1763, p. 617, pl. 25.

Modern form reported from late Pleistocene: Rancho La Brea, Los Angeles, California.

Genus AEGOLIUS Kaup

Aegolius KAUP, Skizz. Entw.-Gesch. Eur. Thierw., 1829, p. 34. Type, by monotypy, *Strix tengmalmi* Gmelin = *Strix funereus* Linnaeus, 1758.

Aegolius funereus (LINNAEUS): Boreal Owl

Strix funerea LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 93.

Modern form reported from Pleistocene:²⁰ Shelter cave, Pyramid Peak, Organ Mountains, Dona Ana County, New Mexico.

¹⁸ *Asio wilsonianus* (Lesson) of the preceding list.

¹⁹ According to a communication from L. H. Miller records formerly cited from Rancho La Brea are erroneous.

²⁰ Possibly of Recent age.

Aegolius acadicus (GMELIN) : Saw-whet Owl

Strix acadica GMELIN, Syst. Nat., vol. 1, pt. 1, 1788, p. 296.

Modern form reported from late Pleistocene: Rancho La Brea, Los Angeles, California. Pleistocene: San Josecito Cave, Aramberri, Nuevo León.

Order CAPRIMULGIFORMES: OILBIRDS, GOATSUCKERS, and ALLIES

Suborder CAPRIMULGI: GOATSUCKERS, POTOOS, and FROGMOUTHS

Family CAPRIMULGIDAE: GOATSUCKERS

Subfamily CAPRIMULGINAE: GOATSUCKERS

Genus PHALAELOPTILUS Ridgway

Phalaenoptilus RIDGWAY, Proc. U. S. Nat. Mus., vol. 3, 1880, p. 5. Type, by original designation, *Caprimulgus nuttallii* Audubon

Phalaenoptilus nuttallii (AUDUBON) : Poor-will

Caprimulgus Nuttalli AUDUBON, Birds Amer., octavo ed., vol. 7, 1844, p. 350, pl. 495.

Modern form reported from Pleistocene: San Josecito Cave, Aramberri, Nuevo León.

Order PICIFORMES: JACAMARS, BARBETS, TOUCANS, and WOODPECKERS

Suborder PICI: WOODPECKERS and WRYNECKS

Family PICIDAE: WOODPECKERS, WRYNECKS, and PICULETS

Subfamily PICINAE: WOODPECKERS

Genus COLAPTES Vigors

Colaptes VIGORS, Trans. Linn. Soc. London, vol. 14, pt. 3, 1826, p. 457. Type, by original designation, *Cuculus auratus* Linnaeus.

Colaptes cafer (GMELIN) : Red-shafted Flicker

Picus cafer GMELIN, Syst. Nat., vol. 1, pt. 1, 1788, p. 431.

Modern form reported from late Pleistocene: Fossil Lake, Oregon; Samwel and Potter Creek caves, Shasta County, Hawver Cave, Eldorado County, McKittrick, Kern County, Carpinteria, Santa Barbara County, and Rancho La Brea, Los Angeles, California.

Colaptes chrysoides (MALHERBE) : Gilded Flicker

Geopicus (Colaptes) chrysoides MALHERBE, Rev. et Mag. Zool., ser. 2, vol. 4, December 1852, p. 553.

Modern form reported from Pleistocene : San Josecito Cave, Aramberri, Nuevo León.

Genus DRYOCOPUS Boie

Dryocopus BOIE, Isis von Oken, Bd. 2, 1826, col. 977. Type, by monotypy, *Picus martius* Linnaeus.

Dryocopus pileatus (LINNAEUS) : Pileated Woodpecker

Picus pileatus LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 113.

Modern form reported from Pleistocene : Cave deposits of Tennessee. Late Pleistocene : Rancho La Brea, Los Angeles, California.

Genus ASYNDESMUS Coues

Asyndesmus COUES, Proc. Acad. Nat. Sci. Philadelphia, vol. 17, No. 1, January-March (June 11), 1866, p. 55. Type, by original designation, *Picus torquatus* Wilson = *Picus lewis* Gray.

Asyndesmus lewis (GRAY) : Lewis' Woodpecker

Picus Lewis GRAY, Gen. Birds, vol. 3, 1849, app., p. 22.

Modern form reported from late Pleistocene : Rancho La Brea, Los Angeles, and Carpinteria, Santa Barbara County, California.

Order PASSERIFORMES : PERCHING BIRDS**Suborder PASSERES : SONG BIRDS****Family ALAUDIDAE : LARKS****Genus EREMOPHILA Brehm**

Eremophila BREHM, Isis, vol. 21, pts. 3-4, 1828, p. 322. Type, by subsequent designation, *Alauda alpestris* Linnaeus (Sharpe, 1890).

Eremophila alpestris (LINNAEUS) : Horned Lark

Alauda alpestris LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 166.

Modern form reported from late Pleistocene : McKittrick and Rancho La Brea, Los Angeles, California.

Family PALAEOSPIZIDAE : PALAEOSPIZA**Genus PALAEOSPIZA Allen**

Palaeospiza ALLEN, Bull. Geol. Geogr. Surv. Terr., vol. 4, No. 2, May 3, 1878, p. 443. Type, by monotypy, *Palaeospiza bella* Allen.

Palaeospiza bella ALLEN

Palaeospiza bella ALLEN, Bull. Geol. Geogr. Surv. Terr., vol. 4, No. 2, May 3, 1878, p. 443, pl. 1, figs. 1-2.

Oligocene (Florissant lake beds):²¹ Florissant, Colorado.

Family HIRUNDINIDAE: SWALLOWS

Genus PETROCHELIDON Cabanis

Petrochelidon CABANIS, Mus. Hein., vol. 1, October (after Oct. 23), 1851, p. 47. Type, by subsequent designation, *Hirundo melanogaster* Swainson (Gray, 1855).

Petrochelidon pyrrhonota (VIEILLOT): Cliff Swallow

Hirundo pyrrhonota VIEILLOT, Nouv. Dict. Hist. Nat., nouv. éd., vol. 14, September 1817, p. 519.

Modern form reported from late Pleistocene: McKittrick, California.

Family CORVIDAE: JAYS, MAGPIES, and CROWS

Subfamily GARRULINAE: JAYS and MAGPIES

Genus CYANOCITTA Strickland

Cyanocitta STRICKLAND, Ann. Mag. Nat. Hist., ser. 1, vol. 15, No. 98, April 1845, p. 261. Type, by original designation, *Corvus cristatus* Linnaeus.

Cyanocitta stelleri (GMELIN): Steller's Jay

Corvus stelleri GMELIN, Syst. Nat., vol. 1, pt. 1, 1788, p. 370.

Modern form reported from late Pleistocene: Samwel Cave, Shasta County, Hawver Cave, Eldorado County, Rancho La Brea, Los Angeles, and Carpinteria, Santa Barbara County, California.

Genus APHELOCOMA Cabanis

Aphelocoma CABANIS, Mus. Hein., vol. 1, sign. 28, Oct. 15, 1851, p. 221. Type, by subsequent designation, *Garrulus californicus* Vigors (Baird, 1858).

Subgenus APHELOCOMA Cabanis

Aphelocoma coerulescens (BOSC): Scrub Jay²²

Corvus coerulescens BOSC, Bull. Soc. Sci. Philom. Paris, vol. 1, pt. 1, 1795, p. 87.

²¹ Recent studies indicate that the age may be Oligocene.

²² Recorded as *Aphelocoma californica* (Vigors), California Jay, in the preceding check-list.

Modern form reported from late Pleistocene: McKittrick, Kern County, Carpinteria, Santa Barbara County, and Rancho La Brea, Los Angeles, California.

Genus PICA Brisson

Pica BRISSON, Orn., 1760, vol. 1, p. 30; vol. 2, p. 35. Type, by tautonymy,
Pica Brisson = *Corvus pica* Linnaeus.

***Pica nuttallii* (AUDUBON): Yellow-billed Magpie**

Corvus nuttallii AUDUBON, Birds Amer. (folio), vol. 4, 1836, pl. 362, fig. 1.

Modern form reported from late Pleistocene: Carpinteria, Santa Barbara County, and Rancho La Brea, Los Angeles, California.

Subfamily CORVINAE: CROWS and RAVENS

Genus CORVUS Linnaeus

Corvus LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 105. Type, by tautonymy,
Corvus = *Corvus corax* Linnaeus.

***Corvus corax* LINNAEUS: Common Raven²³**

Corvus Corax LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 105.

Modern form reported from late Pleistocene: Fossil Lake, Oregon; Hawver Cave, Eldorado County, Carpinteria, McKittrick, Rancho La Brea, Los Angeles, and Playa del Rey (Palos Verdes sand), Los Angeles County, California. Pleistocene: San Josecito Cave, Aramberri, Nuevo León.

***Corvus cryptoleucus* COUCH: White-necked Raven**

Corvus cryptoleucus COUCH, Proc. Acad. Nat. Sci. Philadelphia, vol. 7, No. 2, May 20, 1854, p. 66.

Modern form reported from late Pleistocene: McKittrick and Rancho La Brea, Los Angeles, California.

***Corvus brachyrhynchos* BREHM: Crow**

Corvus brachyrhynchos C. L. BREHM, Beitr. Vögelkunde, vol. 2, 1822, p. 56.

Modern form reported from Pleistocene: Seminole Field, Pinellas County, Florida. Late Pleistocene: Potter Creek Cave, Shasta County, and Rancho La Brea, Los Angeles, California.²⁴

²³ *Corvus shufeldti* Sharpe is a synonym of *C. corax*. See Howard, Carnegie Inst. Washington Publ. 551, Jan. 25, 1946, p. 189.

²⁴ Record formerly given from Carpinteria refers to *C. caurinus*.

Corvus caurinus BAIRD: Northwestern Crow

Corvus caurinus BAIRD, Rep. Expl. and Surv. R. R. Pac., vol. 9, 1858, pp. 559, 569.

Modern form reported from late Pleistocene: Carpinteria, Santa Barbara County, and Rancho La Brea, Los Angeles, California.

Corvus ossifragus WILSON: Fish Crow

Corvus ossifragus WILSON, Amer. Orn., vol. 5, 1812, p. 27, pl. 37, fig. 2.

Modern form reported from Pleistocene: Seminole Field, Pinellas County, Florida.

Corvus pumilis WETMORE

Corvus pumilis WETMORE, Proc. Biol. Soc. Washington, vol. 33, Dec. 30, 1920, p. 81, pl. 2, figs. 3, 4.

Recent (extinct):²⁵ Cave deposits in Cueva San Miguel (type locality), near Morovís, Puerto Rico; Kitchen midden at Concordia, near Southwest Cape, St. Croix, Virgin Islands.

Genus GYMNORHINUS Wied

Gymnorhinus WIED, Reise Nord-Amer., vol. 2, 1841, p. 21. Type, by monotypy, *Gymnorhinus cyanocephalus* Wied.

Gymnorhinus cyanocephalus WIED: Piñon Jay

Gymnorhinus cyanocephalus WIED, Reise Nord-Amer., vol. 2, 1841, p. 22.

Modern form reported from Pleistocene: Conkling Cavern, Pyramid Peak, Organ Mountains, Dona Ana County, New Mexico.

Family SITTIDAE: NUTHATCHES**Subfamily SITTINAE: TYPICAL NUTHATCHES****Genus SITTA Linnaeus**

Sitta LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 115. Type, by monotypy, *Sitta europaea* Linnaeus.

Sitta canadensis LINNAEUS: Red-breasted Nuthatch

Sitta canadensis LINNAEUS, Syst. Nat., ed. 12, vol. 1, 1766, pp. 176, 177.

Modern form reported from late Pleistocene: Carpinteria, Santa Barbara County, California.

²⁵ Included here as it has not been found in living form, being known only from bones. Probably this small crow existed until modern times near Lares, Puerto Rico.

Sitta pygmaea VIGORS: Pygmy Nuthatch

Sitta pygmaea VIGORS, in Zool. Beechey's Voy., 1839, p. 25, pl. 4, fig. 2.

Modern form reported from late Pleistocene: Carpinteria, Santa Barbara County, California.

Family CHAMAEIDAE: WREN-TITS**Genus CHAMAEA Gambel**

Chamaca GAMBEL, Proc. Acad. Nat. Sci. Philadelphia, vol. 3, No. 7, January-February (May 7), 1847, p. 154. Type, by original designation, *Parus fasciatus* Gambel.

Chamaea fasciata (GAMBEL): Wren-tit

Parus fasciatus GAMBEL, Proc. Acad. Nat. Sci. Philadelphia, vol. 2, No. 10, July-August (Dec. 5), 1845, p. 265.

Modern form reported from late Pleistocene: Carpinteria, Santa Barbara County, California.

Family MIMIDAE: THRASHERS and MOCKINGBIRDS**Genus TOXOSTOMA Wagler**

Toxostoma WAGLER, Isis von Oken, vol. 24, Heft 5 (May) 1831, col. 528. Type, by monotypy, *Toxostoma vetula* Wagler = *Orpheus curvirostris* Swainson.

Toxostoma bendirei (COUES): Bendire's Thrasher

Harporhynchus bendirei COUES, Amer. Nat., vol. 7, No. 6, June 1873, p. 330.

Modern form reported from late Pleistocene: McKittrick, Kern County, California.

Toxostoma redivivum (GAMBEL): California Thrasher

Harpes rediviva GAMBEL, Proc. Acad. Nat. Sci. Philadelphia, vol. 2, No. 10, July-August (Dec. 5), 1845, p. 264.

Modern form reported from late Pleistocene: Rancho La Brea, Los Angeles, California.

Genus OREOSOPTES Baird

Oreoscoptes BAIRD, in Baird, Cassin, and Lawrence, Rep. Expl. Surv. R. R. Pac., vol. 9, 1858, pp. XIX, XXXV. Type, by monotypy, *Orpheus montanus* Townsend.

Oreoscoptes montanus (TOWNSEND): Sage Thrasher

Orpheus montanus TOWNSEND, Journ. Acad. Nat. Sci. Philadelphia, vol. 7, pt. 2, Nov. 21, 1837, p. 192.

Modern form reported from late Pleistocene: McKittrick, Kern County, and Rancho La Brea, Los Angeles, California.

Family TURDIDAE: THRUSHES

Genus **TURDUS** Linnaeus

Turdus LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 168. Type, by subsequent designation, *Turdus viscivorus* Linnaeus (Gray, 1840).

Turdus migratorius LINNAEUS: Robin

Turdus migratorius LINNAEUS, Syst. Nat., ed. 12, vol. 1, 1766, p. 292.

Modern form reported from late Pleistocene: Carpinteria, Santa Barbara County, California.

Genus **SIALIA** Swainson

Sialia SWAINSON, Philos. Mag., n. s., vol. 1, No. 5, May 1827, p. 369. Type, by monotypy, *Sialia azurea* Swainson = *Motacilla sialis* Linnaeus.

Sialia mexicana SWAINSON: Western Bluebird

Sialia mexicana SWAINSON, Fauna Bor.-Amer., vol. 2, 1831 (February, 1832), p. 202.

Modern form reported from late Pleistocene: Carpinteria, Santa Barbara County, California.

Family BOMBYCILLIDAE: WAXWINGS

Genus **BOMBYCILLA** Vieillot

Bombycilla VIEILLOT, Hist. Nat. Ois. Amér. Sept., vol. 1, 1807 (1808), p. 88. Type, by monotypy, *Bombycilla cedrorum* Vieillot.

Bombycilla cedrorum VIEILLOT: Cedar Waxwing

Bombycilla cedrorum VIEILLOT, Hist. Nat. Ois. Amér. Sept., vol. 1, 1807 (1808), p. 88, pl. 57.

Modern form reported from late Pleistocene: Carpinteria, Santa Barbara County, and Rancho La Brea, Los Angeles, California.

Family LANIIDAE: SHRIKES

Subfamily LANIINAE: SHRIKES

Genus **LANIUS** Linnaeus

Lanius LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 93. Type, by subsequent designation, *Lanius excubitor* Linnaeus (Swainson, 1824).

Lanius ludovicianus LINNAEUS: Loggerhead Shrike

Lanius ludovicianus LINNAEUS, Syst. Nat., ed. 12, vol. 1, 1766, p. 134.

Modern form reported from late Pleistocene: McKittrick, Kern County, and Rancho La Brea, Los Angeles, California.

Family ICTERIDAE: MEADOWLARKS, BLACKBIRDS, and TROUPIALS**Genus STURNELLA Vieillot**

Sturnella VIEILLOT, Analyse, 1816, p. 34. Type, by monotypy, Stourne, ou Merle à fer-à-cheval Buffon = *Alauda magna* Linnaeus.

Sturnella neglecta AUDUBON: Western Meadowlark

Sturnella neglecta AUDUBON, Birds Amer., octavo ed., vol. 7, 1844, p. 339, pl. 489.

Modern form reported from late Pleistocene: Carpinteria, McKittrick, Rancho La Brea, Los Angeles, and San Pedro (Palos Verdes formation), Los Angeles County, California.

Genus AGELAIUS Vieillot

Agelaius VIEILLOT, Analyse, 1816, p. 33. Type, by subsequent designation, Troupiale commandeur Buffon = *Oriolus phoeniceus* Linnaeus (Gray, 1840).

Agelaius phoeniceus (LINNAEUS): Red-winged Blackbird

Oriolus phoeniceus LINNAEUS, Syst. Nat., ed. 12, vol. 1, 1766, p. 161.

Modern form reported from Pleistocene: Seminole Field, Pinellas County, Florida.

Genus EUPHAGUS Cassin

Euphagus CASSIN, Proc. Acad. Nat. Sci. Philadelphia, vol. 18, No. 5, November-December, 1866 (July 20, 1867), p. 413. Type, by monotypy, *Psarocolius cyanocephalus* Wagler.

Euphagus cyanocephalus (WAGLER): Brewer's Blackbird ²⁶

Psarocolius cyanocephalus WAGLER, Isis von Oken, vol. 22, Heft 7 (July), 1829, col. 758.

Modern form reported from late Pleistocene: Fossil Lake, Oregon; McPherson County, Kansas (Kentuck locality).

²⁶ The record by L. H. Miller from the Pleistocene of Hawver Cave, Eldorado County, California (Univ. California Publ. Geol., vol. 6, Oct. 28, 1911, pp. 399, 400), was subsequently questioned by the same author (Condor, 1921, p. 130). In recent correspondence A. H. Miller writes that he has examined the material reported on from this cave and does not find this species represented. It is therefore omitted from the list. *Euphagus affinis* Shufeldt is a synonym of *E. cyanocephalus*.

Euphagus magnirostris MILLER

Euphagus magnirostris A. H. MILLER, Univ. California Publ., Bull. Dept. Geol. Sci., vol. 19, No. 1, Dec. 21, 1929, p. 14, pl. 1, figs. *f*, *h*.

Late Pleistocene: Rancho La Brea, Los Angeles, California.

Genus CASSIDIX Lesson

Cassidix LESSON, Traité d'Orn., livr. 6, Feb. 1, 1831, p. 433. Type, by subsequent designation, *Cassidix mexicanus* Lesson = *Corvus mexicanus* Gmelin (Gray, 1840).

Cassidix mexicanus (GMELIN): Boat-tailed Grackle

Corvus mexicanus GMELIN, Syst. Nat., vol. 1, pt. 1, 1788, p. 375.

Modern form reported from Pleistocene: Seminole Field, Pinellas County, Florida.

Genus QUISCALUS Vieillot

Quiscalus VIEILLLOT, Analyse, 1816, p. 36. Type, by subsequent designation, *Gracula quiscula* Linnaeus (Gray, 1840).

Quiscalus quiscula (LINNAEUS): Grackle

Gracula Quiscula LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 109.

Modern form reported from Pleistocene: Seminole Field, Pinellas County, Florida.

Genus PYELORHAMPHUS Miller

Pyelorhamphus A. H. MILLER, Auk, vol. 49, No. 1, January 1932, p. 39. Type, by original designation, *Pyelorhamphus molothroides* Miller.

Pyelorhamphus molothroides MILLER

Pyelorhamphus molothroides A. H. MILLER, Auk, vol. 49, No. 1, January 1932, p. 39, pl. 4.

Quaternary (? Pleistocene): ²⁷ Shelter Cave, Pyramid Peak, Organ Mountains, Dona Ana County, New Mexico.

Genus PANDANARIS Miller

Pandanaris A. H. MILLER, Condor, vol. 49, No. 1, Feb. 6, 1947, p. 22. Type, by original designation, *Pandanaris convexa* A. H. Miller.

Pandanaris convexa MILLER

Pandanaris convexa A. H. MILLER, Condor, vol. 49, No. 1, Feb. 6, 1947, p. 22, fig. 4 a-d.

Late Pleistocene: Pit "A," Rancho La Brea, Los Angeles, California.

²⁷ The deposits in which this extinct species was found are possibly of Recent age.

Family FRINGILLIDAE: GROSBEAKS, FINCHES, SPARROWS, and BUNTINGS

Subfamily RICHMONDENINAE: CARDINALS and ALLIES

Genus PHEUCTICUS Reichenbach

Phœucticus REICHENBACH, Av. Syst. Nat., June 1, 1850, pl. 78. Type, by subsequent designation, *Pitylus aureoventris* Lafresnaye and d'Orbigny (Gray, 1855).

Pheucticus melanocephalus (SWAINSON): Black-headed Grosbeak

Guiraca melanocephala SWAINSON, Philos. Mag., n. s., vol. 1, No. 6, June 1827, p. 438.

Modern form reported from late Pleistocene: Rancho La Brea, Los Angeles, California.

Subfamily CARDUELINAE: PURPLE FINCHES, GOLDFINCHES, and ALLIES

Genus HESPERIPHONA Bonaparte

Hesperiphona BONAPARTE, Consp. Gen. Avium, vol. 1, sign. 64, 1850 (Feb. 3, 1851), p. 505. Type, by original designation, *Fringilla vespertina* W. Cooper.

Hesperiphona vespertina (COOPER): Evening Grosbeak

Fringilla vespertina W. COOPER, Ann. Lyc. Nat. Hist. New York, vol. 1, pt. 2, 1825, p. 220.

Modern form reported from late Pleistocene: Rancho La Brea, Los Angeles, California.

Genus CARPODACUS Kaup

Carpodacus KAUP, Skizz. Entw.-Gesch. Eur. Thierw., 1829, p. 161. Type, by subsequent designation, *Loxia rosea* Pallas (Gray, 1842).

Subgenus BURRICA Ridgway

Burrica RIDGWAY, Man. North Amer. Birds, 1887, p. 390. Type, by original designation, *Fringilla mexicana* Müller.

Carpodacus mexicanus (MÜLLER): House Finch

Fringilla mexicana P. L. S. MÜLLER, Natursyst., Suppl., 1776, p. 165.

Modern form reported from late Pleistocene: McKittrick, Kern County, California.

Genus SPINUS Koch

Spinus KOCH, Syst. Baier. Zool., vol. 1, 1816, p. 233. Type, by tautonymy,
Fringilla spinus Linnaeus.

Spinus pinus (WILSON): Pine Siskin

Fringilla pinus WILSON, Amer. Orn., vol. 2, 1810, p. 133, pl. 17, fig. 1.

Modern form reported from Pleistocene: Carpinteria and Rancho La Brea, Los Angeles, California.

Spinus tristis (LINNAEUS): American Goldfinch

Fringilla tristis LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 181.

Modern form reported from late Pleistocene: Rancho La Brea, Los Angeles, California.

Genus LOXIA Linnaeus

Loxia LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 171. Type, by subsequent designation, *Loxia curvirostra* Linnaeus (Gray, 1840).

Loxia curvirostra LINNAEUS: Red Crossbill

Loxia Curvirostra LINNAEUS, Syst. Nat., ed. 10, vol. 1, 1758, p. 171.

Modern form reported from late Pleistocene: Carpinteria, Santa Barbara County, California.

Subfamily EMBERIZINAE: SPARROWS and BUNTINGS**Genus PALAEOSTRUTHUS Wetmore**

Palaeostruthus WETMORE, Bull. Mus. Comp. Zoöl., vol. 67, May 1925, p. 192.
Type, by original designation, *Palaeospiza hatcheri* Shufeldt.

Palaeostruthus hatcheri (SHUFELDT)

Palaeospiza hatcheri SHUFELDT, Bull. Amer. Mus. Nat. Hist., vol. 32, art. 16,
Aug. 4, 1913, p. 301, pl. 55, fig. 28.

Middle Pliocene: Near Long Island, Kansas.

Genus PIPILO Vieillot

Pipilo VIEILLOT, Analyse, 1816, p. 32. Type, by monotypy, Pinson aux yeux rouges Buffon = *Fringilla erythrophthalma* Linnaeus.

Pipilo maculatus SWAINSON: Spotted Towhee

Pipilo maculata SWAINSON, Philos. Mag., n. s., vol. 1, 1827, p. 434.

Modern form reported from late Pleistocene: Rancho La Brea, Los Angeles, and Carpinteria, California.

Pipilo fuscus SWAINSON: Brown Towhee

Pipilo fusca SWAINSON, Philos. Mag., n. s., vol. 1, 1827, p. 434.

Modern form reported from late Pleistocene: Rancho La Brea, Los Angeles, and Carpinteria, California.

Pipilo angelensis DAWSON

Pipilo angelensis DAWSON, Condor, vol. 50, No. 2, Mar. 16, 1948, p. 39, fig. 16.

Late Pleistocene: Rancho La Brea, Los Angeles, California.

Genus CALAMOSPIZA Bonaparte

Calamospiza BONAPARTE, Geogr. and Comp. List, 1838, p. 30. Type, by monotypy, *Fringilla bicolor* J. K. Townsend = *Calamospiza melanocorys* Stejneger.

Calamospiza melanocorys STEJNEGER: Lark Bunting

Calamospiza melanocorys STEJNEGER, Auk, vol. 2, No. 1, January 1885, p. 49.

Modern form reported from late Pleistocene: Meade County, Kansas (Jones fauna, Vanhem formation).

Genus AMMODRAMUS Swainson

Ammodramus SWAINSON, Philos. Mag., n. s., vol. 1, No. 6, June 1827, p. 435.

Type, by monotypy, *Ammodramus bimaculatus* Swainson.

Ammodramus savannarum (GMELIN): Grasshopper Sparrow

Fringilla savannarum GMELIN, Syst. Nat., vol. 1, pt. 2, 1789, p. 921. (Jamaica).

Modern form reported from Pleistocene: Near Haile, 4 miles north-east of Newberry, Alachua County, Florida.

Genus POOECETES Baird

Poecetes BAIRD, in Baird, Cassin, and Lawrence, Rep. Expl. Surv. R. R. Pac., vol. 9, 1858, pp. xx, xxxix. Type, by monotypy, *Fringilla graminea* Gmelin.

Poecetes gramineus (GMELIN): Vesper Sparrow

Fringilla graminea GMELIN, Syst. Nat., vol. 1, pt. 2, 1789, p. 922.

Modern form reported from Pleistocene: Rancho La Brea, Los Angeles, California.

Genus CHONDESTES Swainson

Chondestes SWAINSON, Philos. Mag., n. s., vol. 1, No. 6, June 1827, p. 435.

Type, by monotypy, *Chondestes strigatus* Swainson.

Chondestes grammacus (SAY): Lark Sparrow

Fringilla grammaca SAY, in Long, Exped. Rocky Mts., vol. 1, 1823, p. 139.

Modern form reported from late Pleistocene: Rancho La Brea, Los Angeles, California.

Genus AMPHISPIZA Coues

Amphispiza COUES, Birds Northwest, 1874, p. 234. Type, by original designation, *Emberiza bilineata* Cassin.

Amphispiza bilineata (CASSIN): Black-throated Sparrow

Emberiza bilineata CASSIN, Proc. Acad. Nat. Sci. Philadelphia, vol. 5, No. 5, September-October (Dec. 7), 1850, p. 104, pl. 3.

Modern form reported from late Pleistocene: Rancho La Brea, Los Angeles, California.

Amphispiza belli (CASSIN): Bell's Sparrow

Emberiza Belli CASSIN, Proc. Acad. Nat. Sci. Philadelphia, vol. 5, No. 5, September-October (Dec. 7), 1850, p. 104, pl. 4.

Modern form reported from late Pleistocene: McKittrick, Kern County, and Rancho La Brea, Los Angeles, California.

Genus SPIZELLA Bonaparte

Spizella BONAPARTE, Giornale Arcadico, vol. 52, October-December 1831 (1832), p. 205. Type, by monotypy, *Fringilla pusilla* Wilson.

Spizella passerina (BECHSTEIN): Chipping Sparrow

Fringilla passerina BECHSTEIN, in Latham, Allgem. Uebers. Vögel, vol. 3, pt. 2, 1798, p. 544, pl. 120, fig. 1.

Modern form reported from late Pleistocene: Rancho La Brea, Los Angeles, California.

Genus ZONOTRICHIA Swainson

Zonotrichia SWAINSON, in Swainson and Richardson, Fauna Bor.-Amer., vol. 2, 1831 (February 1832), p. 493. Type, by subsequent designation, *Fringilla pensylvanica* Latham = *Fringilla albicollis* Gmelin (Bonaparte, 1831).

Zonotrichia leucophrys (FORSTER): White-crowned Sparrow

Emberiza leucophrys J. R. FORSTER, Philos. Trans., vol. 62, art. 29, 1772, p. 426.

Modern form reported from late Pleistocene: Rancho La Brea, Los Angeles, California.

Genus **PASSERELLA** Swainson

Passerella SWAINSON, Nat. Hist. and Class. Birds, vol. 2, July 1, 1837, p. 288.
Type, by monotypy, *Fringilla iliaca* Merrem.

Passerella iliaca (MERREM) : Fox Sparrow

Fringilla iliaca MERREM, Avium Rar. Icones et Descrip., vol. 2, 1786, p. 37,
pl. 10.

Modern form reported from late Pleistocene: Rancho La Brea, Los Angeles, and Carpinteria, California.

Genus **MELOSPIZA** Baird

Melospiza BAIRD, in Baird, Cassin, and Lawrence, Rep. Expl. Surv. R. R. Pac., vol. 9, 1858, pp. xx, xl, 440, 476. Type, by original designation, *Fringilla melodia* Wilson.

Subgenus **MELOSPIZA** Baird

Melospiza melodia (WILSON) : Song Sparrow

Fringilla melodia WILSON, Amer. Orn., vol. 2, 1810, p. 125, pl. 16, fig. 4.

Modern form reported from late Pleistocene: Rancho La Brea, Los Angeles, California.

INCERTAE SEDIS

Genus **CIMOLOPTERYX** Marsh ²⁸

Cimolopteryx MARSH, Amer. Journ. Sci., ser. 3, vol. 38, 1889, p. 83, footnote. Type, by monotypy, *Cimolopteryx rarus* Marsh.

Cimolopteryx rarus MARSH

Cimolopteryx rarus MARSH, Amer. Journ. Sci., ser. 3, vol. 38, July 1889, p. 83, footnote.

Upper Cretaceous (Lance formation) : Niobrara County, Wyoming.

Cimolopteryx retusus MARSH

Cimolopteryx retusus MARSH, Amer. Journ. Sci., ser. 3, vol. 44, August 1892, p. 175.

Upper Cretaceous (Lance formation) : Niobrara County, Wyoming.

²⁸ Lambrecht, Handb. Palaeorn., 1933, pp. 586-587, lists this genus at the end of the Ichthyornithiformes. He suggests that the two species belong in separate genera, possibly in different families. See also Shufeldt, Trans. Connecticut Acad. Arts Sci., vol. 19, February 1915, pp. 11, 12, and 76.

Genus **EOPTERYX** Meyer

Eopteryx MEYER, Ber. Senckenberg. Nat. Ges. Frankfurt am Main, 1887, p. 14. Type, by monotypy, *Eopteryx mississippiensis* Meyer.

Eopteryx mississippiensis MEYER²⁹

Eopteryx mississippiensis MEYER, Ber. Senckenberg. Nat. Ges. Frankfurt am Main, 1887, p. 14, pl. 2, figs. 22a-22c.

Eocene: Jackson, Mississippi.

(Genus uncertain)

Falco falconellus SHUFELDT³⁰

Falco falconella SHUFELDT, Trans. Connecticut Acad. Arts Sci., vol. 19, February 1915, p. 40, pl. 15, figs. 139-143.

Eocene (Bridger formation): Dry Creek?, Wyoming.

Genus **FONTINALIS** Lesquereux

Fontinalis LESQUEREUX, Rep. U. S. Geol. Surv. Terr., vol. 8, 1883, p. 135. Type, by monotypy, *Fontinalis pristina* Lesquereux.

Fontinalis pristina LESQUEREUX³¹

Fontinalis pristina LESQUEREUX, Rep. U. S. Geol. Surv. Terr., vol. 8, 1883, p. 135, pl. 21, fig. 9.

Oligocene (Florissant lake beds): Florissant, Colorado.

Genus **HEBE** Shufeldt

Hebe SHUFELDT, Journ. Geol., vol. 21, October-November (Nov. 1), 1913, p. 644. Type, by monotypy, *Hebe schucherti* Shufeldt.

Hebe schucherti SHUFELDT³²

Hebe schucherti SHUFELDT, Journ. Geol., vol. 21, October-November (Nov. 1), 1913, p. 644, fig. 10, a, b.

Eocene:³³ 5 miles west of Green River, Wyoming.

²⁹ Described from a fragmentary vertebra.

³⁰ Not a falcon; relationships doubtful. See Wetmore, A., Proc. U. S. Nat. Mus., vol. 84, Nov. 3, 1936, pp. 77-78.

³¹ Type a fragment of a fossil feather, described originally as a species of moss. See Knowlton, Proc. U. S. Nat. Mus., vol. 51, Nov. 24, 1916, p. 245, and Wetmore, Bull. Mus. Comp. Zool., vol. 67, May 1925, p. 184. Possibly of Oligocene age.

³² Said to be a passeriform bird with four notches in the posterior border of the sternum; of uncertain affinity. *Hebe* Shufeldt, 1913, is preoccupied by *Hebe* Risso, 1826 (applied to a genus of crustaceans), so that should the form here under consideration be definitely identified it may require a new generic appellation. There is no necessity for action at this time in view of its uncertain relationships.

³³ From data furnished by Dr. M. R. Thorpe, of the Peabody Museum, Yale University.

Genus IGNOTORNIS Mehl

Ignotornis MEHL, Amer. Journ. Sci., ser. 5, vol. 21, May 1931, p. 443. Type, by monotypy, *Ignotornis mcconnelli* Mehl.

***Ignotornis mcconnelli* MEHL ³⁴**

Ignotornis mcconnelli MEHL, Amer. Journ. Sci., ser. 5, vol. 21, May 1931, p. 444, fig. 1.

Cretaceous (Dakota sandstone): About 1½ miles northwest of Golden, Colorado.

Genus LAOPTERYX Marsh

Laopteryx MARSH, Amer. Journ. Sci., ser. 3, vol. 21, April 1881, p. 341. Type, by monotypy, *Laopteryx priscus* Marsh.

***Laopteryx priscus* MARSH ³⁵**

Laopteryx priscus MARSH, Amer. Journ. Sci., ser. 3, vol. 21, April 1881, p. 341.

Upper Jurassic (Morrison formation): Quarry 9, Como Bluff, southern Wyoming.

Genus LAORNIS Marsh

Laornis MARSH, Amer. Journ. Sci., ser. 2, vol. 49, March 1870, p. 206. Type, by monotypy, *Laornis edwardsianus* Marsh.

***Laornis edwardsianus* MARSH ³⁶**

Laornis edwardsianus MARSH, Amer. Journ. Sci., ser. 2, vol. 49, March 1870, p. 206.

Paleocene (Hornerstown marl): Near Birmingham, New Jersey.

Genus PALAEONORNIS Emmons

Palaconornis EMMONS, Amer. Geol., pt. 6, 1857, p. 148. Type, by monotypy, *Palaconornis struthionoides* Emmons.

***Palaconornis struthionoides* EMMONS ³⁷**

Palaconornis Struthionoides EMMONS, Amer. Geol., pt. 6, 1857, p. 148, fig. 114.

? Triassic: Anson County, North Carolina.

³⁴ Described from fossil impressions of 4-toed footprints, apparently with webs connecting the three anterior toes.

³⁵ J. D. Dana, Amer. Journ. Sci., ser. 5, vol. 12, July 1926, pp. 3, 4, considered the avian affinity of this supposed species as not definitely certain.

³⁶ Doubtfully related to Anseriformes. Lambrecht, Handb. Palaeorn., 1933, pp. 526-527, has placed it uncertainly after the Aramidæ.

³⁷ Affinity doubtful: possibly not avian.

Genus UINTORNIS Marsh

Uintornis MARSH, Amer. Journ. Sci., ser. 3, vol. 4, October 1872, p. 259.

Type, by monotypy, *Uintornis lucaris* Marsh.

***Uintornis lucaris* MARSH ³⁸**

Uintornis lucaris MARSH, Amer. Journ. Sci., ser. 3, vol. 4, October 1872, p. 259.

Eocene (Bridger formation) : Near Henry's Fork, Wyoming.

Genus YALAVIS Shufeldt

Yalavis SHUFELDT, Journ. Geol., vol. 21, October-November (Nov. 1), 1913, p. 649. Type, by monotypy, *Yalavis tenuipes* Shufeldt.

***Yalavis tenuipes* SHUFELDT ³⁹**

Yalavis tenuipes SHUFELDT, Journ. Geol., vol. 21, October-November (Nov. 1), 1913, p. 649, figs. 11c and 12c.

Geologic age and locality of occurrence not known.

³⁸ According to Shufeldt, Trans. Connecticut Acad. Arts Sci., vol. 19, February 1915, pp. 50-52, 77, pl. 6, fig. 42, this species is of uncertain affinity, and is not a woodpecker as suggested by Marsh.

³⁹ Said in the original description to be a passeriform bird of uncertain affinity.

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PALEOCENE MAMMALIAN FAUNAS OF THE
BISON BASIN IN SOUTH-CENTRAL
WYOMING

(WITH 16 PLATES)

By

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Charles D. and Mary Vaux Walcott Research Fund

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BISON BASIN IN SOUTH-CENTRAL
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By C. LEWIS GAZIN

*Curator, Division of Vertebrate Paleontology
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(WITH 16 PLATES)

INTRODUCTION

One of the more interesting developments relative to the investigation of early Tertiary mammals in the Rocky Mountain region during the past several years was the discovery in 1952 by Dr. R. W. Brown, Harold Masursky, and H. R. Christner of the U. S. Geological Survey of the occurrence of Paleocene mammal remains in the Bison basin of Wyoming. The Bison basin is in the Sweetwater drainage to the north of the Red Desert, and its south rim forms part of the Continental Divide, separating inland drainage of the Continental Divide basin from that of the Missouri River system. The gray and buff to reddish silty clays and sandstones of the Paleocene are here exposed at intervals along the escarpment bounding the basin. There are four principal fossil localities—two in the exposures below the south rim of the basin, one in the southwestern part, and one at the western extremity. These have been determined as lying within sections 28 and 29 of T. 27 N., R. 95 W., in Fremont County, but very near the southern boundary.

Slight differences in age would appear to be indicated by the faunas represented at the different localities, but most if not all may be included within the early or lower part of Tiffanian upper Paleocene. Similarities to the Torrejonian fauna of the Montana Fort Union are noted, but these are in part attributed to a possible similarity in rather general environmental conditions. A resemblance is evident in the variety of carnivores and condylarths, modified by certain genera which are regarded as indicative of Tiffanian time.

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In addition to the Geological Survey personnel above mentioned as having discovered the occurrence of Paleocene mammals in the Bison basin, acknowledgment is due George N. Pipiringos, James MacLachlan, Dr. J. R. Hough, and Robert DeMar for having given field aid in 1953. Dr. Paul O. McGrew aided in turning over, for the purposes of this study, collections obtained for the University of Wyoming in 1953. Particular mention may be made of interest shown in this work by Dr. Roland W. Brown in having first called my attention to the occurrence, and in his marked contribution to the field collecting in both 1952 and 1953, as well as being an original discoverer.

Acknowledgment is made of aid no less important from Drs. George G. Simpson, Edwin H. Colbert, Bobb Schaeffer, and Mrs. Rachel H. Nichols in permitting me to examine and make comparisons with various Paleocene collections in the American Museum and from Dr. Glenn L. Jepsen in making available type and other materials in the extensive Polecat Bench Paleocene collections at Princeton University.

The drawings depicting the specimens shown in plates I to II were made by Lawrence B. Isham; those of *Caenolambda pattersoni* in plates 12 to 14 by William D. Crockett.

HISTORY OF INVESTIGATION

Following discovery of the fossil materials by the U. S. Geological Survey party in July 1952¹ and their reference to me for study and report, the results of a preliminary examination were presented before the Cambridge meeting of the Society of Vertebrate Paleontology in November. During the later part of 1952 and early in 1953, Wallace G. Bell, a graduate student at the University of Wyoming, engaged in a thesis study of the geology of a rather general area including the Bison basin, and Paul McGrew made collections at certain of the fossiliferous sites. Agreement was early reached whereby the University of Wyoming party would join with the Smithsonian Institution-U. S. Geological Survey expedition in the search of these exposures in the summer of 1953, and that I would be permitted to study and describe the collections as a whole.

In June 1953 a party from Washington consisting of Dr. Roland W. Brown, Franklin Pearce, and myself was accompanied in the field by Messrs. Pipiringos and MacLachlan. We were joined at the fossil

¹ A very cursory examination of these beds was made by the writer in 1951, accompanied by C. L. Jenks, Jr., of the Shell Oil Co., but on the north side of the basin where exposures are evidently quite barren of fossils.

locality by Dr. Hough and Mr. DeMar of the U. S. Geological Survey and by Dr. McGrew and his party of students from the University. The combined efforts of the group were largely concentrated in a search of the vicinity of the small saddle or discovery locality below the south rim of the basin, and a site found by Mr. Bell in the south-western part of the basin. Later, a third fossiliferous site was encountered by Dr. Brown, Mr. Pearce, and myself at the western extremity of the basin, and Pearce located a fourth along a ledge on the south escarpment between the saddle and Bell's *Titanoides* locality.

All sites were revisited by Pearce and me with continued success in 1954 but with diminishing returns, as it appears that the original richness of the sites was due largely to a residual concentration of materials, and the interval between successive field seasons is evidently too short for erosion to afford profitable collecting. Moreover, there seemed to be no one place where the concentration of bone might be regarded as great enough to warrant quarrying operations.

OCCURRENCE AND PRESERVATION OF MATERIAL

The four principal fossil occurrences (see pls. 15 and 16) are referred to in the following discussion as the saddle or discovery locality, the ledge locality, Bell's or the *Titanoides* locality, and the west-end locality. The small badland saddle where Brown and others of the Geological Survey first encountered bone is located about mid-way north and south in the eastern half of sec. 28, T. 27 N., R. 95 W., according to information from Bell's mapping furnished me by McGrew. The richest concentration of the smaller forms was in the saddle, determined by means of a hand level to be about 58 feet below the rim or top of the escarpment immediately to the south. The beds here have a dip of approximately 9° southward. Fossils were found scattered for about a couple of hundred feet in either direction from the saddle and stratigraphically near the same level, although a couple of specimens of *Plesiadapis jepseni* in the University of Wyoming collections came from possibly 50 feet higher. The material rather generally consists of incomplete jaws and maxillae and a good number of isolated teeth. A single skull, that of the new pantodont *Caenolambda pattersoni*, was encountered in a nodule a little distance away but at about the stratigraphic level of the saddle.

Approximately a quarter of a mile or more to the west, apparently in the western half of section 28, a northwest-facing exposure exhibits a prominent ledge about 25 or 30 feet below the rim. A fair concentration of jaw and maxillary portions and isolated teeth was found for a hundred feet or less along the ledge and in the soft clay

for a few feet immediately above. The ledge locality would seem almost certainly to be stratigraphically much higher than the saddle. The locality is nearer the rim, hence topographically higher, and the dip of the beds may be a little more southwesterly than at the saddle so that the ledge would appear to be stratigraphically higher than any portion of the escarpment above the saddle. A considerable extent, however, of the exposures between the two localities is obscured by talus and vegetation, and so the relationship could not be determined precisely.

The locality that I am informed Mr. Bell discovered, and from which the University of Wyoming secured upper teeth of *Titanoides primaevus*, is still farther west, about midway north and south in the eastern half of adjacent section 29. The general locality is in the southwestern part of the basin and just west of the most westerly of the wagon trails crossing the south rim of the basin. Fossils, though comparatively few, were found ranging from very near the top of the escarpment to 30 or 40 feet stratigraphically lower. The beds here appear to have a greater southerly dip than at the saddle or ledge localities, and the stratigraphic position relative to the more easterly localities is not readily evident from field relations, as much of the escarpment between this locality and the ledge is obscured. The faunas discussed in the following part of this paper would suggest that it is still higher.

The most westerly locality is an east-facing gravel-capped exposure at the west end of the basin, evidently about midway east and west across section 29, close to the northern line. Fossils were discovered here in a very restricted zone around a low hill set out from near the base of the exposure and at about its most southeasterly extent. Jaws and isolated teeth were encountered over an area of only a few hundred square feet on the slopes extending out from the base of this hill. The west-end exposure is well isolated by grass and sagebrush slopes from the *Titanoides* locality to the south, but there seems no doubt from the dip at the latter locality that the west-end site must be considerably lower stratigraphically, unless the intervening rock is complicated by changes in dip or faulting. The relative position of the horizon represented with respect to that at the ledge or saddle is uncertain, but there is some evidence from the fossils that it may not be far removed in time from that represented at the ledge.

THE BISON BASIN FAUNAS

The following tabulation pertains to the four principal localities in the Bison basin from which collections were obtained. The figures

used refer to the number of specimens encountered, giving an indication of the extent of the material upon which identifications are based, as well as some, though generally meager, information on the relative abundance of the various forms within and between the faunas. In certain instances species names are repeated but on a less certain or comparative basis where differences of a minor sort, possibly variant or subspecific in value, are noted between related materials from two different localities.

From the tabulated data it is seen that the known collections total about 236 generally determinable specimens. Of these 53 are in the collections of the University of Wyoming, with occurrence divided between the vicinity of the saddle and the *Titanoides* locality. The larger collections are in the U. S. National Museum and represent all four sites.

	Saddle loc.	Ledge loc.	West-end loc.	<i>Titanoides</i> loc.
REPTILIA:				
Sauria:				
Anguid, undet.	6	1
MAMMALIA:				
Multituberculata:				
Cf. <i>Ptilodus montanus</i> Douglass.....	1
Cf. <i>Ectypodus musculus</i> Matthew and Granger....	1
Cf. <i>Ectypodus hazeni</i> Jepsen.....	1
Cf. <i>Anconodon russelli</i> (Simpson).....	1
Marsupialia:				
<i>Peradectes elegans</i> Matthew and Granger.....	1
<i>Peradectes pauli</i> , new species.....	2
Insectivora:				
<i>Diacodon pearcei</i> , new species.....	1
<i>Bisonalveus browni</i> , new genus and species.....	4
Primates:				
<i>Pronothodectes</i> , cf. <i>matthewi</i> Gidley.....	4
<i>Pronothodectes simpsoni</i> , new species.....	..	9
<i>Pronothodectes</i> , cf. <i>simpsoni</i> , new species.....	8
<i>Plesiadapis</i> , cf. <i>fodinatus</i> Jepsen.....	..	1	2	3
<i>Plesiadapis jepseni</i> , new species.....	11*	7	2	..
<i>Plesiadapis</i> , cf. <i>jepseni</i> , new species.....	2
Carnivora:				
<i>Tricentes fremontensis</i> , new species.....	11	2
<i>Chriacus</i> , near <i>C. pelvidens</i> (Cope).....	3	..	1	..
<i>Chriacus</i> , sp. (small).....	1
<i>Thryptacodon</i> , cf. <i>australis</i> Simpson.....	1	1
<i>Thryptacodon demari</i> , new species.....	..	6	1	..
<i>Thryptacodon</i> , cf. <i>demari</i> , new species.....	2	..	1	1
<i>Thryptacodon belli</i> , new species.....	11	..	1	..

MAMMALIA—continued

Carnivora—continued

	Saddle loc.	Ledge loc.	West-end loc.	<i>Titanoides</i> loc.
<i>Claenodon</i> , cf. <i>procyonoides</i> (Matthew).....	3
<i>Claenodon</i> , cf. <i>montanensis</i> (Gidley).....	5
<i>Claenodon</i> , cf. <i>ferox</i> (Cope).....	5	..	3	1
<i>Claenodon acrogenius</i> , new species.....	6	1
<i>Dissacus</i> , sp.	2
<i>Didymictis</i> , near <i>D. tenuis</i> Simpson.....	1

Condylarthra:

<i>Promioclænus pippingosi</i> , new species.....	1
Cf. <i>Promioclænus pippingosi</i> , new species.....	..	2
<i>Promioclænus</i> ? sp.	1
<i>Litomylus scaphicus</i> , new species.....	2	1
<i>Litomylus scaphiscus</i> , new species.....	1	2
<i>Haplaletes pelicatus</i> , new species.....	4
<i>Haplaletes serior</i> , new species.....	1
<i>Protoselene</i> ? <i>novissimus</i> , new species.....	2
<i>Litolestes lacunatus</i> , new species.....	1	3
Cf. <i>Litolestes lacunatus</i> , new species.....	1
<i>Gidleyina wyomingensis</i> , new species.....	..	10	9	..
<i>Gidleyina</i> , cf. <i>wyomingensis</i> , new species.....	5	3
<i>Phenacodus</i> ? <i>bisonensis</i> , new species.....	28	2
<i>Phenacodus</i> ? sp. (large).....	..	1	1	2

Pantodonta:

<i>Titanoides primaevus</i> Gidley.....	1
<i>Caenolambda pattersoni</i> , new genus and species....	1
Cf. <i>Caenolambda pattersoni</i> , new genus and species.	1	1
Pantodont, undet. (tooth frags.).....	2	5	3	1

* Two of these are from the vicinity of the saddle locality but approximately 50 feet higher.

ENVIRONMENT AND RELATIONSHIPS BETWEEN THE
BISON BASIN FAUNAS

Although differences are noted between the faunas represented at the four principal localities, all four faunas appear to be Tiffanian, and for the most part, if not all, a comparatively early part of this time interval. Whether these differences are essentially a matter of chance collecting, of facies or environmental differences with time as a minor factor, or of change resulting in part from evolution of certain persisting kinds, but complicated by migration involving the introduction and disappearance or local extinction of others, is not entirely clear. Each, though, is likely to have contributed to the picture.

Chance collecting is unquestionably an important factor where the number of specimens of each form is small, but it cannot be predicted with any assurance that further collecting would increase the faunal

resemblance between sites or further emphasize dissimilarities. Undoubtedly certain missing forms would appear, increasing the number of genera and species common to two or more localities, but better representation of populations of each would likely point out persistent differences.

A stratigraphic difference seems evident between at least three of the four sites so that differences due to environment or facies would not be unexpected, whereas this would be unlikely were the same horizon represented at each in so restricted a geographic area. Chance collecting may be appealed to as distorting the picture with respect to environmental differences, particularly where the numbers of specimens are small; nevertheless, with the same collecting personnel involved at each of the sites, attention may be directed to certain contrasting features observed. The saddle locality for example shows evidence of a fauna containing a wealth of smaller mammalian forms. Scant numbers of specimens show a variety of multituberculates, marsupials, and insectivores not represented at the other localities. Still better materials include representation of primates, creodonts, and condylarths, with equivalent or closely related forms known at the other levels. Almost all the genera here peculiar to the saddle locality, with the exception of *Bisonalveus* and *Protoselene*?, are elsewhere known in later faunas, so that one may postulate in addition to time an environmental difference possibly only of local significance which, were it not for the persistence of the primates, would suggest a more open or less sylvan environment for the later levels. The saddle genera missing from the higher levels I suspect are forest-dwelling types. On the other hand, all but two, *Dissacus* and *Titanoides*, of the genera known in the four faunas as a whole are represented in the saddle collections, indicative of a cosmopolitan assemblage of a type perhaps better known only from the Crazy Mountain Fort Union and evidently also from the Polecat Bench. In all probability the Torrejon fauna is of a more open terrain, although points of resemblance are seen in the Carnivora. Nevertheless, the condylarths in particular and many of the other forms from the Bison basin seem more closely allied to faunas of the Crazy Mountain Fort Union as well as to those of the Polecat Bench series. No doubt much of this resemblance is regional in significance and perhaps generally characteristic of the extensive Fort Union, which the Wyoming as well as the Montana sites have been regarded as representing. These in turn are geographically remote with a rather distinctive difference in latitude from the Nacimiento deposits in the San Juan basin of New Mexico.

There would seem to be little doubt that some differences observed between the Bison basin faunas may be attributed to time. That there is a time difference seems evident from the stratigraphic relations, and the localities in the foregoing tabulation are arranged from left to right in ascending order as far as I can determine, except that the relative position of the west end with respect to the ledge locality is entirely uncertain. The more marked differences between the various localities, such as in the genera represented, would, between what appear to be closely related faunas, have less significance as a time factor than the differences observed between the most closely related types. Change resulting from the evolution of certain forms, or the superseding of primitive by more advanced though related types, may be noted in at least three of the orders.

Among the primates *Pronothodectes* is represented in both the saddle and ledge localities, but evidently not higher, and the more primitive *Pronothodectes matthewi* has been found only at the saddle level. *Plesiadapis* is recognized at all localities, and the smaller of these, *P. jepseni*, is best or more typically represented at the saddle and ledge, whereas large *P. cf. fodinatus* has not been found in the saddle and most of the material is from the presumably highest or *Titanoides* locality.

Among the Carnivora, *Tricentes* was encountered frequently at the saddle, scantily at the ledge and not higher. Particularly striking with regard to the change in Carnivora is the development of *Thryptacodon*. The small *T. belli* found in the saddle is replaced at the ledge by distinctly larger *T. demari*, almost certainly through development in situ. Material of *Thryptacodon*, which appears structurally a little different than the foregoing and resembling more closely *T. australis*, is found only at the west-end and *Titanoides* localities, although associated there with scant materials that appear to indicate one or both of the other species. These latter, however, may possibly represent variation within a population of a single species in which the mean is rapidly changing. On the other hand, *T. australis* may have appeared from elsewhere during the later time here represented. The impressive display in range of size for *Claenodon* is seen only at the saddle, and only the typically large form compared to *Claenodon ferox* and possibly a single specimen of *Claenodon acrogenius* occur at higher levels. It is possible that *Tricentes* and the smaller forms of *Claenodon* may have become extinct during the interval included by the Bison basin faunas.

Most of the small condylarths are found only in the saddle or ledge faunas, and there appears in these no comment-worthy differences be-

tween the two faunas; however, a single specimen of *Haplaletes* encountered at the *Titanoides* locality is of a surprisingly larger form than the *Haplaletes* represented at the saddle. On the other hand, a single specimen from the saddle referred tentatively to *Litolestes lacunatus* is scarcely different than the typical material from the *Titanoides* locality. Among the larger condylarths the form described as *Gidleyina wyomingensis* from the ledge and west-end localities may be a little more progressive than indicated by material referred to it from the saddle. Abundant *Phenacodus?* *bisonensis* is almost restricted to the saddle level although two specimens came from the ledge. This seems replaced by a considerably larger, at the same time much more rare, species from the ledge and higher. The span of time represented by the Bison basin faunas may have witnessed the extinction of such forms as *Promioclænus* (which includes much that had been grouped before under *Ellipsodon*), *Protoselene*, and *Litomylus*.

It is not known to what extent the times of *Caenolambda* and *Titanoides* may have overlapped. Typical materials of each were found as single specimens at the saddle and *Titanoides* localities respectively. Undetermined pantodont tooth fragments were collected at all localities.

AGE AND CORRELATION OF THE FAUNAS

In consideration of the age or ages represented by the Bison basin faunas we may deal first with that represented at the saddle locality, rather clearly the oldest of the four levels. In regarding this as Tiffanian somewhat greater emphasis is given to the appearance of forms known to characterize later horizons than to the presence or survival of older genera. For example, *Plesiadapis*, *Thryptacodon*, *Litolestes*, *Gidleyina*, and *Phenacodus* may be regarded as Tiffanian in first appearance, whereas *Pronothodectes*, *Tricentes*, *Clænodon*, *Promioclænus*, *Litomylus*, *Haplaletes*, and *Protoselene* have been rather generally thought to be Torrejonian. Species represented of certain of the latter genera are not clearly separable from those of the Torrejonian levels in the Nacimiento and Fort Union and might be regarded as long lived, but others in this group such as *Pronothodectes simpsoni*, *Clænodon acrogenius*, *Litomylus scaphicus*, and *Haplaletes pelicatus* are distinctly advanced.

The interpretation that there is an admixture of materials of rather different horizons at the saddle locality, though not impossible, may be discarded as a serious possibility inasmuch as nearly all the genera of both aspects are found together at the ledge locality where collecting was limited to a narrow zone above a ledge and very near the top of the escarpment. Moreover, among the Tiffanian genera repre-

sented at the saddle an early stage of development seems clearly indicated in *Plesiadapis jepseni*, *Thryptacodon belli*, and the material referred to *Gidleyina wyomingensis*, as well as in the close approach that *Phenacodus? bisonensis* makes to *Tetraclaenodon*.

With due regard to the presence of forms of older aspect in the fauna an age assignment of early or lower Tiffanian rather than later Torrejonian seems indicated. This is further supported by the resemblance or similarity that persists between the Bison basin faunas, although above the saddle and particularly above the ledge locality the Torrejonian aspects appear to be lost. Direct comparison of the saddle fauna with that of the Melville is difficult because of the sparsity of Carnivora and condylarths so well represented in the Bison basin; nevertheless the saddle level may not be much older than the Melville, generally regarded as lower Tiffanian.

The fauna from the *Titanoides* locality is rather limited, but evidence is seen for a somewhat more typical Tiffanian stage. The presence of *Titanoides primaevus* suggests a definite relationship only with a horizon in the type Fort Union in western North Dakota, although somewhat smaller forms from the Melville and Silver Coulee have been referred to this genus, as well as "*Sparactolambda*" *looki* from the DeBeque beds. A large species of *Plesiadapis* regarded as closest to *P. fodinatus* from the Silver Coulee level of the Polecat Bench series suggests an equivalent horizon in Tiffanian time, but the Bison basin form in at least one individual retains a second lower premolar not seen in any of the typical *P. fodinatus* material. Material close to *Plesiadapis jepseni* also occurs at the *Titanoides* locality, suggesting a closer tie with the older levels in the Bison basin. The *Thryptacodon* here is evidently to be compared closely with that from the Tiffany beds in Colorado. The presence of *Claenodon* cf. *ferox* is not significant in view of the still later occurrence of this genus in beds of Clarkforkian age elsewhere. *Haplaletes serior* would possibly suggest a comparatively early horizon, but this species is so much larger than that from the Lebo, or even than the form described from the saddle locality in the Bison basin, that its significance seems lost. *Litolestes* is a Tiffanian genus here represented by a species which appears to differ only in being of larger size than that from the Melville and much larger than the Silver Coulee genotype. *Gidleyina* and the material of the comparatively large form of *Phenacodus?* at the *Titanoides* locality suggest little other than Tiffanian.

From the foregoing it would seem that the *Titanoides* locality fauna, in the absence of forms of Torrejonian aspect, might be regarded as somewhat higher in the Tiffanian than Melville but, from consideration of the primates only, possibly not so late as Silver Coulee.

Except for their intermediate positions, no particular additional evidence is forthcoming from the ledge and west-end locality faunas, other than that the ledge would seem almost certainly closer to the saddle than to the *Titanoides* locality in age.

SYSTEMATIC DESCRIPTION OF VERTEBRATE REMAINS

REPTILIA

SAURIA

ANGUIDAE

The only nonmammalian specimens encountered during the collecting were four fragmentary dentaries, two portions of maxillae, and a premaxilla of a lizard. These were examined by Dr. David H. Dunkle and recognized as belonging to a small anguid type. The genus represented could not be determined from the material at hand, but *Peltosaurus* has been recognized in horizons as early as Lance and Fort Union. Nevertheless *Glyptosaurus* and *Xestops* also include diminutive species and these genera are known in the Eocene. All but one of the specimens came from the saddle locality. A single fragmentary dentary was found at the *Titanoides* locality.

MAMMALIA

MULTITUBERCULATA

PTILODONTIDAE

Although the multituberculates appear to be comparatively rare, to judge by the frequency with which their remains are encountered, nevertheless they must have been highly diversified, because each of the four fragmentary specimens known evidently represents a different form. The materials in each case are too incomplete to indicate with certainty the genus represented but, of the forms tentatively identified, two suggest Torrejonian and two Tiffanian, although three of the specimens came from the small saddle locality discovered by Dr. R. W. Brown. The fourth specimen, that compared with the Tiffanian *Ectypodus musculus*, came from a short distance away but regarded as the same stratigraphic horizon as the saddle.

Cf. *PTILODUS MONTANUS* Douglass, 1908

Plate 1, figure 1

A relatively large ptilodont multituberculate is represented by a single incomplete left P₄, U.S.N.M. No. 20877. There is no certainty

that the form represented is *Ptilodus*, as no other portions of the dentition were found and the anterior margin of the tooth was broken away. In size and outline, as well as in the spacing of the serrations, of which there were at least 13, the tooth rather closely resembles P_4 in *Ptilodus montanus*. The preserved portion measures 8.1 mm., but estimated from complete specimens of *P. montanus* this tooth in its entirety would have been about 8.8 or 8.9 mm. long and within the upper limit of measurements for *P. montanus*.

Cf. ECTYPODUS MUSCULUS Matthew and Granger, 1921

Plate 1, figure 3

A small jaw fragment with M_1 and the alveoli for M_2 , U. of Wyo. No. 1105, would appear to represent *Ectypodus musculus*. The size of the included molar, 2.5 by 1.25 mm., is near that given by Granger and Simpson (1929, p. 655) for *E. musculus*, although the Wyoming specimen would appear to be about a quarter of a millimeter broader. The cusp formula, 9: 5 or 6, is comparable to the 8:6 cited by Jepsen (1940, p. 307) as well as by Matthew and Granger, particularly as one of the outer cusps in No. 1105 is scarcely distinct. This tooth may well belong to the form represented by the P_4 , U.S.N.M. No. 20878, compared below with *Ectypodus hazeni* but is appreciably shorter than the 3.2 mm. cited by Jepsen for the length of M_1 in *E. hazeni*, although the cusp formula for this tooth is the same as that for *E. musculus*.

Cf. ECTYPODUS HAZENI Jepsen, 1940

Plate 1, figure 2

An isolated though complete P_4 , U.S.N.M. No. 20878, compares very closely to this tooth in the Silver Coulee *Ectypodus hazeni*. It resembles this form in the size (5 mm. long) and outline of the tooth but has only 11, or possibly 12, serrations rather than the 13 listed by Jepsen (1940, p. 307). No. 20878 also resembles P_4 in *Mimetodon churchilli*, which is indicated as having 12 serrations, but the tooth has perhaps a somewhat more convex profile, with the straight posterior section a relatively shorter part of the entire profile. The anterior margin of the tooth is deeply notched and pocketed, suggesting the presence of P_3 , but the absence of other associated material precludes certain generic identification.

Cf. *ANCONODON RUSSELLI* (Simpson), 1935

Plate 1, figure 4

Anconodon russelli may be represented by a fragment of the right mandibular ramus showing the root portion of the incisor and P_4 , U. of Wyo. No. 1065. The preserved premolar is close in size to that referred above to *Ectypodus hazeni*, but its profile is slightly more convex dorsally and has a long straight front edge more as in *Anconodon*. P_4 is 5.2 mm. in length, which is about midway in the range of 4.9 to 5.4 mm. given by Jepsen (1940, p. 291) for *Anconodon russelli*. The number of serrations is not certainly determined but would appear to be about 13 or 14. Fourteen serrations are noted for several of the Gidley Quarry specimens from the Crazy Mountain Fort Union, but 15 or 16 prevail in the Rock Bench material according to Jepsen.

MARSUPIALIA

DIDELPHIDAE

PERADECTES ELEGANS Matthew and Granger, 1921

Plate 2, figure 6

A rather well preserved right mandibular ramus with the posterior three molars, U. of Wyo. No. 1104, corresponds so closely in direct comparison with the type of *Peradectes elegans* from the Tiffany of Colorado that there seems no doubt that the species are the same. Lower molars are, of course, amazingly conservative in didelphids, but the near identity in various measurements of the teeth in the Bison basin jaw and the type leave no alternative but recognition of this species in the upper Paleocene of Wyoming. Measurements of the teeth have been incorporated below with those of the following species believed to be distinct.

PERADECTES PAULI,² new species

Plate 2, figures 4, 5

Type.—Portion of left mandibular ramus with last two molars, U.S.N.M. No. 20879.

Horizon and locality.—Bison basin Tiffanian, saddle locality, below south rim of Bison basin, sec. 28, T. 27 N., R. 95 W., Fremont County, Wyo.

Specific characters.—Appreciably smaller teeth than *Peradectes elegans* and lower molars with outer cusps slightly less elevated and talonids relatively more abbreviated.

² Named for Paul O. McGrew.

Discussion.—In addition to being of smaller size than *Peradectes elegans*, it was noted that lower molars of *P. pauli* show a protoconid which, though higher than the paraconid and metaconid, is not so much elevated with respect to these cusps. Also, the hypoconid is a comparatively lower cusp. Moreover, the talonid basin is relatively both a little narrower and shorter than in *P. elegans* and the entoconid and hypoconulid a little less widely separated.

With the distinctions between species of didelphid marsupials generally including little more than size so far as characters of lower molars are concerned and with very limited information on the variability of observed structural differences in these earlier forms, conclusions as to generic identity based on lower molars are not entirely satisfactory. As to whether the cited differences preclude reference of *P. pauli* to *Peradectes* there is no certainty. Although the somewhat lower protoconid might suggest *Peratherium*, this is not supported by the more abbreviated talonids, and the entoconid is not nearly so prominent. Furthermore, *Peratherium* has not been certainly recognized in pre-Eocene deposits. In the absence of any representation of the upper dentition, about which on a generic level evidence of a somewhat more satisfactory nature has been developed (Simpson, 1935a), the species is assigned to *Peradectes*.

MEASUREMENTS IN MILLIMETERS OF LOWER TEETH IN SPECIES OF *Peradectes*

	<i>Peradectes elegans</i>		<i>Peradectes pauli</i> , n. sp.	
	A.M.N.H. No. 17376 (type)	U. of Wyo. No. 1104	U.S.N.M. No. 20879 (type)	U.S.N.M. No. 20880
M ₁ , anteroposterior diameter	1.75	1.6
transverse diameter of trigonid.....	0.9	0.7
transverse diameter of talonid.....	0.95	0.75
M ₂ , anteroposterior diameter	1.75	1.7
transverse diameter of trigonid.....	1.0	1.0	...	0.8
transverse diameter of talonid.....	1.0	1.0
M ₃ , anteroposterior diameter	1.75	1.7	1.55	...
transverse diameter of trigonid.....	1.05	1.05	0.95	...
transverse diameter of talonid.....	1.05	1.0	0.8	...
M ₄ , anteroposterior diameter	1.75	1.65	1.6	...
transverse diameter of trigonid.....	0.95	0.95	0.85	...
transverse diameter of talonid.....	0.8	0.7	0.6	...

INSECTIVORA
LEPTICTIDAE

Simpson (1937b) presented a logical arrangement of the earlier leptictids which went far toward clarifying the complexity and diversity of these forms. Nevertheless, a review of the various mate-

rials in connection with the study of the leptictid form represented in the Bison basin Paleocene has indicated the need for certain further modification.

Attention (Gazin, 1952) was called to the rather distinctive characters observed in the type of *Diacodon alticuspis*, and I am now convinced that Cope's *Ictops bicuspis* should not have been referred to *Diacodon* and that Matthew's earlier disposition of this species under the name *Palaeictops* should be revived. As well as *Palaeictops bicuspis* (Cope), this genus apparently should include *Palaeictops tauricineri* (Jepsen) and *Palaeictops pineyensis* (Gazin) from among the lower Eocene forms, and possibly also *Palaeictops minutus* (Jepsen) from the Silver Coulee (Tiffanian) Paleocene.

The genus *Prodiacodon* was named by Matthew as a subgenus replacing *Palaeolestes* (preoccupied) for the species *P. puercensis* of the Torrejon horizon. This form, though generically distinct, is, I believe, more closely allied to *Palaeictops bicuspis* than to typical *Diacodon* or *D. alticuspis*. In 1935 Simpson (see 1937b) described *Prodiacodon concordiarzensis* from the upper Lebo (Torrejonian) and expressed some doubt as to the correctness of referring it to that genus. In view of the somewhat later but closely related form encountered in the Bison basin fauna, and of the particular characteristics, rather generally overlooked, of *Diacodon alticuspis*, I am placing both the Lebo and Bison basin forms in *Diacodon*. These then become *Diacodon concordiarzensis* (Simpson) and *Diacodon pearcei*, new species.

DIACODON PEARCEI,³ new species

Plate 1, figure 6

Type.—Left ramus of mandible with P₃-M₁, U.S.N.M. No. 20970.

Horizon and locality.—Bison basin Tiffanian, small saddle below south rim of Bison basin, sec. 28, T. 27 N., R. 95 W., Fremont County, Wyo.

Specific characters.—*Diacodon pearcei* closely resembles *Diacodon concordiarzensis* (Simpson) from the Crazy Mountain Fort Union (upper Lebo) in the structure of the teeth, but is distinctly larger, about intermediate between *D. concordiarzensis* and *D. alticuspis*. P₄ is seen to be about 14 percent longer and 27 percent wider than in *D. concordiarzensis* and about 20 percent shorter and 22 percent narrower than *D. alticuspis*. The paraconid of this tooth is higher than in the Lebo species.

³ Named for Franklin L. Pearce.

Discussion.—The closeness of the resemblance between *D. concordiacensis* and *D. pearcei* convinces me that whatever disposition is made of one, so far as the genus is concerned, the other must likewise be assigned. These two are characterized by comparatively high trigonids and abbreviated molar talonids, associated with a progressive P_4 , with a likewise abbreviated though basined talonid. The combination of characters seems most closely approximated in the San Jose and Knight material of *Diacodon alticusps*. In *Palaeictops* P_4 is comparable in progressiveness, but the talonid in this tooth and in the lower molars is broad and long, comprising a greater proportion of the tooth crown. The molar trigonids, though also high in certain species, are relatively shorter anteroposteriorly. *Prodiacodon* is likewise characterized by comparatively large talonids. A small cuspule about halfway down the posterior slope of P_2 and P_3 in *Prodiacodon puericensis* and much better developed in species of *Palaeictops* is not seen on the P_2 of *D. concordiacensis* or the P_3 of *D. pearcei*. On the other hand, an anterior cuspule, well developed and high on these teeth in the latter two species, is absent or weak and low in *Prodiacodon* and *Palaeictops*.

Among the other early leptictids, *Leptacodon* has a less progressive P_4 than *Diacodon*, with a strong but low paraconid and in particular a comparatively weak and more posterior metaconid. Moreover, the molar trigonids appear lower and the talonids comparatively larger than in *Diacodon*. *Myrmecoboides* has a large P_4 with paraconid forward as in *Diacodon* and *Palaeictops*, though lower; however, the greatly elongated talonids exhibited in the molars and P_4 immediately distinguish this genus. The abbreviation of the talonid on P_4 and the lower molars of *Xenacodon* is suggestive of *Diacodon*, but P_4 would appear to be distinctly less progressive in that the paraconid is small and the talonid not basined.

MEASUREMENTS IN MILLIMETERS OF LOWER TEETH IN TYPE SPECIMEN
OF *Diacodon pearcei*, U.S.N.M. NO. 20970

P_3 , anteroposterior diameter : greatest transverse diameter	1.8 : 1.0
P_4 , anteroposterior diameter : transverse diameter of trigonid.....	2.4 : 1.4
M_1 , anteroposterior diameter : transverse diameter of trigonid.....	2.2 : 1.6

PANTOLESTIDAE

BISONALVEUS,⁴ new genus

Type.—*Bisonalveus browni*, new species.

Generic characters.—Resembling *Aphronorus*, but P_4 much smaller

⁴ *Bison* + *alveus*, basin—for Bison basin.

and exhibiting a slightly more noticeable paraconid and a better developed and more posterolingual entoconid. Paraconids of lower molars higher and more lingual, but hypoconulid of M_1 and M_2 indistinct and less prominently projecting on M_3 . Entoconid on M_1 and M_2 more forward in position. Small cuspule on crest anterolingual to hypoconid on M_3 .

Discussion.—The structure of P_4 and the general form of the molars suggest an alliance of this form with *Aphronorus* and hence with the pantolestids, although the weakness of the hypoconulid would seem to negate such a relationship. The molars, though exhibiting comparatively acute cusps, might by themselves have been regarded as condylarth.

P_4 of *Bisonalveus* has a slightly better developed paraconid at the anterolingual margin of tooth, and a more pronounced and posterolingually located entoconid so that this portion of the talonid crest is not so depressed or so nearly oblique. The metaconid is only a little lower than the protoconid and slightly posterior to it. The shape of these two cusps is rather like that in *Aphronorus*.

The lower molars show elevated trigonids, somewhat less so than in *Aphronorus*, but the paraconid is almost as high as the metaconid. The paraconid, moreover, is more lingual in position than it is in *Aphronorus*. The talonids of the molars are basined much as in *Aphronorus*, but the arcuate posterior crest of the first two shows little or no evidence of a hypoconulid. It may be noted that the hypoconulid on molars of *Aphronorus* is relatively weak in comparison with middle Eocene *Pantolestes* but is nevertheless clearly defined. In *Bisonalveus*, furthermore, the entoconid has a more forward position on the crest of the talonid in M_1 and M_2 than in *Aphronorus*. In M_3 the entoconid and hypoconulid are closer together. Anterior to the hypoconid on M_3 (only) there is a distinct cuspule, much as seen in some leptictid molars.

Bisonalveus lower molars differ from those of *Bessoecetor* in much the same way as they do from those of *Aphronorus*. The fourth lower premolar, however, is entirely different from that of *Bessoecetor* and has more nearly the form of that in *Aphronorus*.

BISONALVEUS BROWNI,⁵ new species

Plate 1, figure 5

Type.—Left ramus of mandible with P_4 - M_3 , U.S.N.M. No. 20928.

Horizon and locality.—Bison basin Tiffanian, saddle locality, south

⁵ Named for Dr. Roland W. Brown.

rim of Bison basin, sec. 28, T. 27 N., R. 95 W., Fremont County, Wyo.

Specific characters.—In size of teeth *Bisonalveus browni* is distinctly smaller than *Aphronorus fraudator* Simpson. The length of the lower molar series is about 13 percent shorter, whereas P_4 is about 45 percent less in length, and 36 percent narrower. Specific characters are not otherwise distinguished from those of the genus.

In addition to the type there are in the collections of National Museum a fragmentary left mandibular ramus with M_3 (No. 20929) and an isolated P_4 (No. 20930). A jaw fragment with a much worn P_4 and M_1 in the University of Wyoming collections (No. 1067) may also represent this species.

MEASUREMENTS IN MILLIMETERS OF LOWER TEETH IN TYPE SPECIMEN
OF *Bisonalveus browni*, U.S.N.M. NO. 20928

Length of lower cheek tooth series, P_4 - M_3 , incl.....	9.5
Length of lower molar series, M_1 - M_3 , incl.....	7.5
P_4 , anteroposterior diameter : greatest transverse diameter.....	2.2 : 1.5
M_1 anteroposterior diameter : transverse diameter of trigonid.....	2.5 : 1.7
M_2 anteroposterior diameter : transverse diameter of trigonid.....	2.6 : 2.0
M_3 anteroposterior diameter : transverse diameter of trigonid.....	2.6 : 1.5

PRIMATES

PLESIADAPIDAE

In numbers of jaws and, to a lesser extent, maxillae, the plesiadapids are surprisingly well represented. Not less than four species, presumably divided between two genera, are recognized. Not all, however, are found associated at any one locality. The most primitive, *Pronothodectes* cf. *matthewi*, and presumably the most progressive, *Plesiadapis* cf. *fodinatus*, are not found together, but both are associated with the forms or variants of the forms that might be referred to as intermediate in development, *Pronothodectes simpsoni* and *Plesiadapis jepseni*. *Pronothodectes* is generally regarded as a forerunner of *Plesiadapis*, which it undoubtedly is, but their occurrence together here is unquestionable in two restricted localities. *Pronothodectes* cf. *matthewi* and a small variant of *Pronothodectes simpsoni* are found associated with *Plesiadapis jepseni* at the saddle locality and typical *Pronothodectes simpsoni* is associated with *Plesiadapis jepseni* and *Plesiadapis* cf. *fodinatus* (a single specimen of a small individual) at the stratigraphically much restricted ledge locality. At the more westerly and probably higher localities *Plesiadapis* cf. *fodinatus* is found with scant material referred, perhaps questionably, to *Plesiadapis jepseni*.

PRONOTHODECTES, cf. MATTHEWI Gidley, 1923

Plate 2, figures 1, 2

A decidedly small plesiadapid is represented in the collections by four lower jaw portions and a maxillary fragment. One of the jaws, U.S.N.M. No. 20758, includes P_4 - M_2 and part of M_3 , and a second specimen, U. of Wyo. No. 1062, exhibits P_3 - M_1 . The maxillary portion, U. of Wyo. No. 1099, with two molars, is very tentatively referred but would seem to belong with this material rather than the larger *Pronothodectes simpsoni*.

There is little doubt that the genus represented is *Pronothodectes* rather than *Plesiadapis*, as the dental formula includes all the lower premolars. The species represented is very close to the small *Pronothodectes matthewi*, which Gidley (1923) described from the Montana Fort Union. The lower premolars and molar trigonid cusps, though sloping, are less so than in *Plesiadapis* material of the *P. anceps* type, and the trigonids are moderately compressed anteroposteriorly as in *Pronothodectes matthewi*. Only a slightly greater transverse width to the teeth was noted in the Bison basin material.

All the specimens of this form were obtained from the saddle locality at the south rim of the Bison basin, associated with *Pronothodectes* cf. *simpsoni* and *Plesiadapis jepseni*, but not the advanced *Plesiadapis* cf. *jodinatus*.

MEASUREMENTS IN MILLIMETERS OF TEETH REFERRED TO
Pronothodectes matthewi GIDLEY

		U. of Wyo. No. 1099
M ¹ , anteroposterior diameter		2.5
M ² , anteroposterior diameter		2.5
	U.S.N.M. No. 20758	U. of Wyo. No. 1062
P ₃ , anteroposterior diameter : transverse diameter		1.8 : 1.5
P ₄ , anteroposterior diameter : transverse diameter	2.1 : 1.7	2.2 : 1.8
M ₁ , anteroposterior diameter : transverse diameter of talonid	2.4 : 2.0	2.5 : 2.1
M ₂ , anteroposterior diameter : transverse diameter of talonid	2.5 : 2.3
M ₃ , anteroposterior diameter	3.2 ^a

^a Approximate.PRONOTHODECTES SIMPSONI,⁶ new species

Plate 3

Type.—Right ramus of mandible with P_4 - M_3 , U.S.N.M. No. 20754.

Horizon and locality.—Bison basin Tiffanian, ledge locality at south

⁶ Named for Dr. G. G. Simpson in appreciation of his work on the early primates.

rim of Bison basin, W $\frac{1}{2}$ sec. 28, T. 27 N., R. 95 W., Fremont County, Wyo.

Specific characters.—Size nearly intermediate between *Pronothodectes matthewi* and *Plesiadapis gidleyi*, closer to the latter. P₁ pressed close to incisor, posterior lower premolars and molar trigonids of more inflated appearance than in *P. matthewi*.

Discussion.—The more typical materials of this species are from the ledge locality about a quarter of a mile west of the saddle locality and include about nine jaws besides the type in the collections of the U. S. National Museum. About four specimens in each of the National Museum and University of Wyoming collections from the saddle locality would seem to represent a variant somewhat smaller in size, although evidently closer to this species than to *Pronothodectes matthewi*. None of the material of this species was found at the more westerly and possibly higher horizons in the basin.

Like the material referred to *Pronothodectes matthewi*, that of this species would appear by definition to be *Pronothodectes* rather than *Plesiadapis*, because in all specimens where the dental formula can be determined all the lower premolars were represented, P₁ and P₂ being, of course, single-rooted teeth as in *P. matthewi*. *P. simpsoni*, as noted in the diagnosis, is characterized by much larger teeth, about 18 to 31 percent larger in length of lower molar series in materials from the ledge locality, and possibly as low as 12 to about 24 percent larger than *P. matthewi* in the materials referred to *P. simpsoni* from the saddle locality.

Pronothodectes simpsoni differs from *P. matthewi*, in addition to its greater size, by exhibiting teeth of a more *Plesiadapis*-like appearance. This is noticeable in the more typical materials from the ledge locality in the comparatively inflated appearance of the cusps. Perhaps it is more noticeable in the trigonid, which is distinctly less anteroposteriorly compressed in M₂ and M₃. The variant from the saddle locality overlaps in size range that represented at the ledge locality and is less obviously different from *P. matthewi* in size and appearance of the cusps, but would seem to be closer to *P. simpsoni*. A lower jaw (U. of Wyo. No. 1057, pl. 3, fig. 2) of *P. cf. simpsoni* with P₄ to M₃ from the saddle locality exhibits a disproportionately long M₃ (buccally incomplete), but other specimens with M₃ from the saddle show this tooth to be normally proportioned. M₁ and M₂ in No. 1057 are scarcely distinguished from these two teeth in the smaller specimens of *P. simpsoni* from the ledge (i.e., U.S.N.M. No. 20770, pl. 3, fig. 3).

MEASUREMENTS IN MILLIMETERS OF LOWER TEETH IN SPECIMENS OF
Pronothodectes simpsoni

	U.S.N.M. No. 20754 (type)	U.S.N.M. No. 20770	U. of Wyo. No. 1057 *
Length of lower molar series.....	9.8	8.9	9.4
P ₄ , anteroposterior diameter : transverse diameter	2.5 : 1.9	2.2 : 2.0
M ₁ , anteroposterior diameter : greatest transverse diameter	2.8 : 2.4	2.6 : 2.3	2.5 : 2.1
M ₂ , anteroposterior diameter : greatest transverse diameter	3.1 : 2.8	2.9 : 2.5	2.7 : 2.5
M ₃ , anteroposterior diameter : greatest transverse diameter	4.3 : 2.5	3.6 : 2.2	4.4 : ..

* Small variant but with large M₃

PLESIADAPIS, cf. FODINATUS Jepsen, 1930

Plate 2, figure 3

Three specimens in the collections of the National Museum and three in those of the University of Wyoming are believed to represent the comparatively large plesiadapid that Jepsen (1940) described from the Silver Coulee horizon in the Polecat Bench series of north-western Wyoming. Represented among these are P₄ to M₃, and only one (U. of Wyo. No. 1085) of the specimens is a maxilla, exhibiting M₂ and M₃. The specimens, with one exception, are from the more westerly localities and probably higher stratigraphically than the saddle locality and possibly higher than the ledge. One jaw with teeth a trifle smaller than in the others came from the ledge but is believed to be closer to *Plesiadapis fodinatus* than it is to the new form, *P. jepsoni*.

The teeth in the Bison basin materials referred to *P. fodinatus* correspond so closely to those of the Silver Coulee form that there would seem to be no serious doubt as to the correctness of the assignment. The resemblance is very close in all proportions of the molar teeth, and like *P. fodinatus* the teeth do not show such markedly sloping labial walls as in correspondingly large *Plesiadapis rex* and related *P. anceps*. It was noted, however, that in one of the jaws, which has preserved the alveoli of the anterior cheek teeth, a small P₂ had been present, although there was no evidence of a P₁. P₂ is not present in the type or other observed materials of *P. fodinatus* from the Princeton Quarry but is present in *P. gidleyi* and almost always present, though not invariably so, in the material described below as the new species, *Plesiadapis jepsoni*. Its presence in the Bison basin jaw compared with *P. fodinatus* may not be significant. There is, moreover, a suggestion in this particular jaw of somewhat smaller premolars and a

shorter diastema behind the incisor than in typical *P. fodinatus*. The length of the diastema, though, is uncertain as the bone is incomplete.

MEASUREMENTS IN MILLIMETERS OF TEETH IN SPECIMENS OF *Plesiadapis*, CF.
fodinatus JEPSEN

	U. of Wyo. No. 1085		
M ² , anteroposterior diameter : greatest transverse diameter....	3.8 : 5.9		
M ² , greatest transverse diameter.....	5.5		
		U. of Wyo. No. 1082	U.S.N.M. No. 20783
P ₄ , anteroposterior diameter : greatest			U.S.N.M. No. 20784
transverse diameter	2.6 : 2.2
M ₁ , anteroposterior diameter : greatest			
transverse diameter	3.6 : 2.9	3.2 : 2.9
M ₂ , anteroposterior diameter : greatest			
transverse diameter	3.6 : 3.4	3.9 : 3.6
M ₃ , anteroposterior diameter : greatest			
transverse diameter	5.5 : 3.5

PLESIADAPIS JEPSENI,⁷ new species

Plate 4

Type.—Left ramus of mandible with P₄-M₃, U.S.N.M. No. 20760.

Horizon and locality.—Bison basin Tiffanian, ledge locality at south rim of Bison basin, W $\frac{1}{2}$ sec. 28, T. 27 N., R. 95 W., Fremont County, Wyo.

Specific characters.—Close in size to *Plesiadapis gidleyi* and *Plesiadapis anceps*. P₂ almost always present and hypoconulid portion of talonid of M₃ broad as in *P. gidleyi*. Lower teeth relatively broad with outer walls decidedly sloping as in *P. anceps* and *P. rex*. Conule weak to scarcely discernible on lingual slope of primary cusp of P³ but prominent on P⁴. Mesostyle absent or very weak on upper molars, M³ slightly more expanded posterointernally than in *P. anceps*.

Discussion.—*Plesiadapis jepseni* is one of the better represented forms in the Bison basin collection, exceeded in number of specimens only by *Phenacodus? bisonensis* and *Gidleyina wyomingensis*. About 23 specimens, mostly lower jaws, are for the most part divided between the saddle and ledge localities below the south rim of the basin. Two, however, came from the locality at the west end of the basin and two from near the *Titanoides primaevus* locality in the southwestern part of the basin. Three mandibular portions and one maxilla are in the collections of the University of Wyoming.

⁷ Named for Dr. Glenn L. Jepsen in appreciation of his work on the Plesiadapidae.

A small part of this collection, that secured by Dr. Roland Brown and others, was originally cataloged and described by me in a preliminary unpublished manuscript, as well as in a report to the U. S. Geological Survey, as representing *Plesiadapis anceps*, which it most nearly resembles in the general structure of the lower molars. The resemblance is noticeable in the relative breadth of the teeth and strongly sloping outer walls, a feature also noted in the larger *Plesiadapis rex*. The protoconid in particular has a long posterolateral slope quite unlike *P. gidleyi* and *P. fodinatus* or the later *P. dubius* and *P. rubeyi*. This slope is characteristic of the posterolateral wall of the primary cusp in premolars as well as in the molars of *P. jepseni* and *P. anceps*. *Plesiadapis jepseni* is unlike *P. anceps* and more nearly resembles *P. gidleyi* in the expansion of the posterior portions of the third upper and lower molars. The posterolingual portion of M^3 , though somewhat more expanded than in *P. anceps*, is possibly not so distinctive in this respect as *P. gidleyi*; however, the third lobe or hypoconulid portion of M_3 is generally as much expanded as in *P. gidleyi*. Moreover, in about eight of the lower jaws in which the presence or absence of P_2 can be determined, it is certainly missing in only one. This tooth is apparently not present in *P. anceps*, typical *P. fodinatus*, and later plesiadapids.

MEASUREMENTS IN MILLIMETERS OF TEETH IN SPECIMENS OF
Plesiadapis jepseni

	U.S.N.M. No. 20781	U.S.N.M. No. 20780
Length of cheek tooth series, P^3-M^3	12.4
Length of upper molar series, M^1-M^3	8.5
P^3 , anteroposterior diameter : greatest transverse diameter	2.0 : 2.3	2.1 : 2.5
P^4 , anteroposterior diameter : greatest transverse diameter	2.2 : 3.1	2.3 : 3.1
M^1 , anteroposterior diameter : greatest transverse diameter	2.9 : 4.1	2.8 : 4.0
M^2 , anteroposterior diameter : greatest transverse diameter	3.0 : 4.7	3.0 : 4.6
M^3 , anteroposterior diameter : greatest transverse diameter	2.9 : 3.9
	U.S.N.M. No. 20760 (type)	U.S.N.M. No. 20586
Length of cheek tooth series, P_4-M_3	12.6
Length of lower molar series, M_1-M_3	10.4
P_3 , anteroposterior diameter : greatest transverse diameter	2.4 : 1.9
P_4 , anteroposterior diameter : greatest transverse diameter	2.4 : 2.8	2.5 : 2.4

M ₁ , anteroposterior diameter : greatest transverse diameter	3.0 : 3.0	3.2 : 3.0
M ₂ , anteroposterior diameter : greatest transverse diameter	3.3 : 3.2	3.3 : 3.2
M ₃ , anteroposterior diameter : greatest transverse diameter	4.4 : 2.9

CARNIVORA

ARCTOCYONIDAE

Creodonts are well represented in the collections, comprising a diversity of forms not hitherto recorded in the Tiffanian. Most of the forms are of arctocyonid types, and among these are species of *Tricentes* and *Claenodon*, suggesting affinities with the earlier Torrejonian faunas, together with *Thryptacodon* better known in later horizons. *Chriacus*, having a comparatively great range in geologic time, is represented by a species rather similar but possibly a little more progressive than that of the Torrejon. So far as *Claenodon* is concerned, although the species are difficult to distinguish from those of the Torrejon, undescribed material of the genus has been obtained from Paleocene deposits as late as Clarkforkian, and the presumably descendant *Anacodon* is, of course, found in the lower Eocene.

OXYCLAENINAE

TRICENTES FREMONTENSIS,⁸ new species

Plate 5, figure 4

Type.—Left ramus of mandible with M₁-M₃, U.S.N.M. No. 20582.

Horizon and locality.—Bison basin Tiffanian, saddle locality at south rim of Bison basin, sec. 28, T. 27 N., R. 95 W., Fremont County, Wyo.

Specific characters.—Teeth close in size to those of *Tricentes subtrigonus* but anterior portion of lower dentition reduced, with trigonid of M₁ narrow and premolars smaller.

Discussion.—The above new specific name is proposed with some hesitancy, as the Torrejon species, *Tricentes subtrigonus*, shows an astonishing amount of variation in characters of the lower teeth. Variation in size, relative proportion of teeth, and cusp development makes any attempt at detailed comparison nearly futile. Marked variability was also noted in the material of *Tricentes fremontensis*. Nevertheless, P₃ and P₄, as observed in U.S.N.M. No. 20584, are smaller than in any of the specimens of *T. subtrigonus* I have examined, and in

⁸ Named for Fremont County, Wyo.

the dozen or more other specimens of *T. fremontensis* at hand the relative narrowness of the anterior molars, particularly the trigonid of M_1 , may be distinctive. The type, U.S.N.M. No. 20582, is a comparatively large individual with teeth relatively wider than nearly all others from this locality. Their width, however, in proportion to their length (more evident in M_1), though matched in certain individuals of *T. subtrigonus*, is rather less than the average in the Torrejon materials observed. Other specimens of *T. fremontensis* appear to be outside the range of *T. subtrigonus* in this respect. Moreover, the paraconid on M_2 and M_3 is placed low on the trigonid of lower molars in *T. fremontensis* and is weaker than generally seen in *T. subtrigonus*. In none of the posterior lower molars of the Bison basin form is this cusp so conspicuously developed as it is in so much of the Torrejon material. It should be noted, however, that the difference is one in average for the material at hand, as teeth of *T. subtrigonus* can be found in which there is scarcely a trace of the paraconid on M_3 .

MEASUREMENTS IN MILLIMETERS OF TEETH IN SPECIMENS OF
Tricentes fremontensis

	U.S.N.M. No. 20584
P_3 , anteroposterior diameter : transverse diameter	4.0 : 2.4
P_4 , anteroposterior diameter : transverse diameter	4.5 : 2.9
	U.S.N.M. No. 20582 (type)
M_1 , anteroposterior diameter : transverse diameter of trigonid.....	6.2 : 3.8
M_1 , transverse diameter of talonid.....	4.5
M_2 , anteroposterior diameter : greatest transverse diameter.....	6.4 : 4.9
M_3 , anteroposterior diameter : greatest transverse diameter.....	6.6 : 4.3

CHRIACUS, near *C. PELVIDENS* (Cope), 1881

Plate 5, figures 1, 2

About four fragmentary jaws of a species of *Chriacus* are included in the collections of the National Museum. Unfortunately, only one of these (U.S.N.M. No. 20983) has as many as two complete teeth. The form represented is undoubtedly close to *Chriacus pelvidens* of the Torrejon, with the anteroposterior diameter of the lower teeth about the same as in that species. Their width, however, in two of these is a little greater than in any of the *C. pelvidens* material at hand. Moreover, the metaconid on P_4 , in one of the two specimens that retains this tooth, is distinctly better developed, as it is in small *Spanoxyodon latrunculus*. Although a distinct species of *Chriacus*, or even possibly *Spanoxyodon*, may well be represented here, the evidence is not conclusive and no satisfactory diagnosis can be made.

P₄ in U.S.N.M. No. 20983 measures 6.1 mm. long by 3.7 mm. wide. M₁ in this specimen is 7.3 by 5.4 mm.

An isolated upper molar, probably M² (U.S.N.M. No. 21003), would also appear to represent a species of *Chriacus* about the size of *C. pelvidens*. The outer styles of this tooth are not noticeably developed, but lingually the cingulum carries a prominent hypocone and a likewise prominent though less developed protostyle at the anterolingual margin of the tooth. This tooth measures 6.3 mm. long by 8.8 mm. wide transversely.

CHRIACUS, sp.

Plate 5, figure 3

A single upper molar from the saddle locality, U.S.N.M. No. 21019, presumably M², is much smaller, approximately 25 percent less in general proportions than the M² discussed in the foregoing section. In size it would appear to be more nearly comparable to *Chriacus truncatus*, approximately that of *Thryptacodon belli*. The rectangular appearance of this tooth and the prominence of the anterointernal cusp or protostyle would seem to remove it from consideration as a form of *Thryptacodon*. The tooth measures 5.2 mm. long by 6.3 mm. wide transversely.

THRYPTACODON, cf. AUSTRALIS Simpson, 1935

Plate 6, figure 5

A fragmentary left mandibular ramus, including P₄, M₁, and M₃, in the collection obtained by the University of Wyoming (No. 1076) from the *Titanoides* locality, in details of the teeth closely approximates that of the species of *Thryptacodon* named by Simpson (1935c) from the Tiffany beds of Colorado. The teeth are a trifle larger than in the type as may be seen from the dimension Simpson has given, but the rudimentary condition of the metaconid on P₄ and the prominently isolated hypoconulid on M₃ suggest possibly a closer relationship to *Thryptacodon australis* than to *T. demari* described as new in the following section.

The trigonid of M₃ in U. Wyo. No. 1076 seems rather broadly basined and the paraconid distinctly weak. Moreover, the hypoconulid, in addition to being prominent, is rather distinctly set off from the entoconid, and there is a low crest between the entoconid and hypoconid. The hypoconulid portion of M₃ is believed to be highly variable in *Thryptacodon*, but *T. australis* material observed shows this cusp rather better defined than in much of the Wasatchian

T. antiquus material exhibiting M_3 . A slightly more posteriorward position for the hypoconulid is indicated also for M_1 , somewhat reminiscent of *Chriacus*, though not nearly so distinctive in this respect and, of course, the teeth in general are not nearly so high cusped.

MEASUREMENTS IN MILLIMETERS OF TEETH IN SPECIMEN REFERRED TO

Thryptacodon australis SIMPSON, U. OF WYO. NO. 1076

P_4 , anteroposterior diameter : greatest transverse diameter.....	5.1 : 2.9
M_1 , anteroposterior diameter : greatest transverse diameter.....	6.7 : 4.6
M_3 , anteroposterior diameter : greatest transverse diameter.....	7.1 : 5.3

THRYPTACODON DEMARI,⁹ new species

Plate 6, figures 2, 3

Type.—Right ramus of mandible with P_4 - M_3 , U.S.N.M. No. 20985.

Horizon and locality.—Bison basin Tiffanian, ledge locality at south rim of Bison basin, $W\frac{1}{2}$ sec. 28, T. 27 N., R. 95 W., Fremont County, Wyo.

Specific characters.—Size a little smaller than *Thryptacodon australis*. P_2 isolated by longer diastemata. Metaconid of P_4 much better developed. Proportions of M_1 about as in *T. australis* but posterior molars comparatively short and broad. Hypoconulid of M_3 variable but may be much reduced.

Discussion.—About 11 specimens in the National Museum collections and one or two in the collection made by the University of Wyoming are recognized as pertaining to the new species *Thryptacodon demari*. The lower molar series of this form is only a little shorter than in *Thryptacodon australis* Simpson from the Tiffany beds of Colorado, and on the basis of size alone would probably not be distinct from that species. In many respects *T. demari* shows points of resemblance to the distinctly more robust appearing *T. antiquus*. The lower premolars, though slender, are well spaced anteriorly, more as in *T. antiquus*. P_4 , however, has a better developed metaconid than in either of these. M_1 is about the same size as in more nearly contemporary *T. australis*, but M_2 and M_3 are shorter and relatively broader. In M_3 the shortness may be effected largely by the more reduced hypoconulid in some specimens which, somewhat as illustrated by Matthew for the type of *T. antiquus*, may be more closely joined to the entoconid, and the talonid basin opened posteriorly between the hypoconid and entoconid. In the Bison basin specimen thought to represent *T. australis*, and as evident in Simpson's illustra-

⁹ Named for Robert DeMar, who aided materially in the collecting of 1953.

tion of the type, the talonid basin of M_3 is confined posteriorly by a low crest between the hypoconid and entoconid and the hypoconulid is sharply separated from the entoconid. It should be noted, however, that an approach to this condition is made in certain specimens of *T. demari*, hence possibly not of diagnostic significance.

Differences from *T. antiquus*, in addition to the development of the metaconid on P_4 , include a little less difference in width between M_2 and the trigonid of M_3 , with M_3 relatively much shorter. Moreover, teeth of *Thryptacodon demari* show a cingulum, usually discontinuous, external to the hypoconid, but it appears not to be developed external to the protocone to the extent seen in *T. antiquus*. Also, it is not nearly so expanded posterior to the hypoconid on M_3 .

A fragmentary maxilla, U.S.N.M. No. 20984, referred to this species, has M^1 and M^2 preserved, and a second maxilla, U.S.N.M. No. 20992, has only M^2 . Also, there is an isolated M^1 in the University of Wyoming collection which may represent this species. M^1 exhibits an anteriorly projecting and weakly cusped parastyle. The cingulum is evenly continuous around the anterior and lingual portions of the tooth and the hypocone is a simple conical cusp rising from the cingulum posterointernal to the the protocone. There is no protostyle and there are no particularly distinct accessory cusps adjacent to the hypocone as observed in the Eocene materials. M^2 lacks the distinctive parastyle, and in No. 20984 (but not in No. 20992) there is a very rudimentary protostyle anterolingual to the protocone where the cingulum is somewhat more sharply deflected around the margin of the tooth than in M^1 . As in M^1 , however, there are no clearly distinguishable accessory cusps adjacent to the hypocone.

The right M^2 described by Simpson (1928) as *Thryptacodon pseudarctos* in the Bear Creek Paleocene fauna of southern Montana is larger and apparently has a more robust protocone than in No. 20984 considered to be *Thryptacodon demari*. The type, *T. pseudarctos*, measures 6.9 by 8.6 mm. Measurements of teeth in *T. demari* are included with those of *T. belli*.

THRYPTACODON BELLI,¹⁰ new species

Plate 6, figures 1, 4

Type.—Right ramus of mandible including M_1 - M_3 , U. of Wyo. No. 1045.

¹⁰ Named for Wallace G. Bell, engaged in the geologic mapping of the Bison basin area.

Horizon and locality.—Bison basin Tiffanian, saddle locality at south rim of Bison basin, sec. 28, T. 27 N., R. 95 W., Fremont County, Wyo.

Specific characters.—Length of lower molar series is about 13 per cent less than in the type of *Thryptacodon demari* and lower jaw much shallower. Upper and lower molars similar to those in *T. demari*, except that M_3 is relatively much narrower.

Discussion.—In addition to the type there are two other specimens representing this species in the University of Wyoming collection and about nine in the collections of the National Museum. No difficulty was encountered in distinguishing these materials from that representing *Thryptacodon demari* and upon completing the segregation of the species it was found that all the material except one specimen of *T. belli* was derived from the saddle locality at the south rim, whereas all but two of the specimens of *T. demari* were from the localities farther to the west, and apparently a little higher stratigraphically.

MEASUREMENTS IN MILLIMETERS OF TEETH IN TWO NEW SPECIES OF *Thryptacodon*

	<i>T. demari</i> U.S.N.M. No. 20984	<i>T. belli</i> U.S.N.M. No. 20986
M^1 , anteroposterior diameter buccally : transverse diameter	5.7 : 6.2
M^2 , anteroposterior diameter buccally : transverse diameter	6.5 ^a : 8.0	5.2 : 7.1
	U.S.N.M. No. 20985 (type)	U. of Wyo. No. 1045 (type)
P_4 , anteroposterior diameter : transverse diameter ...	5.2 : 2.7
M_1 , anteroposterior diameter : transverse diameter ...	6.7 : 4.3	5.6 : 3.8
M_2 , anteroposterior diameter : transverse diameter ...	6.2 : 5.3	5.4 : 4.7
M_3 , anteroposterior diameter : transverse diameter ...	6.2 : 4.8	5.3 : 4.0

^a Approximate.

ARCTOCYONINAE

The approximately 30 specimens of clænodonts in the Bison basin collections nearly run the gamut in size of teeth from a little smaller than in *Clænodon procyonoides* to possibly a little larger than in the largest *Clænodon ferox*, as represented in the Torrejon collections. No one, I believe, would seriously contend that a single species is represented, nor does it seem possible to arrange them logically, with the material at hand, into less than about four species. Possibly a larger collection would show a different distribution as to species and would probably represent not more than three. Simpson (1936) has shown, for example, that the amount of material now known from the Torrejon in New Mexico has resolved the complex there into only two

determinable species, the larger of which exhibits a surprising range in size. A complex similar to that in the Bison basin picture is seen in the fewer though distinctly better materials encountered in the Fort Union of the Crazy Mountain field in Montana. Simpson was there faced with the necessity of recognizing five species, but undoubtedly this arrangement would also be somewhat simplified if an adequate sample could be obtained.

Except for the largest form in the Bison basin fauna, there seem to be no characters but size by which the various species may be recognized. Using Simpson's histogram (1937b, fig. 35) for the length of M_2 in the Torrejon materials in the American Museum, I have, in figure 2, added to the number individuals in each size group according to information derived from Torrejon collections in the National Museum, and included a similar histogram for the Bison basin teeth. In the latter, columns are extended by dashed lines in instances where in the absence of M_2 the size of an adjacent molar is indicative of one group or another. Specific assignments made, mostly tentative, are also shown. I rather suspect that with further material a single intermediate group will eventually be indicated where comparison is now made with *C. montanensis* and *C. ferox*, although the pattern shown in the Torrejon materials would suggest great variation in a large species. Nevertheless, the differences between the new species, *C. acrogenius*, and that referred to *C. ferox* are rather marked and would appear to include more than size of teeth alone.

CLAENODON, cf. PROCYONOIDES (Matthew), 1937

Plate 7, figure 5

A decidedly small species of *Claenodon* is represented at the saddle locality by a lower jaw, U.S.N.M. No. 20630, including the molars M_1 - M_3 , a jaw portion retaining only P_2 and P_3 , U.S.N.M. No. 21007, and an isolated M_3 . The proportions of the teeth in No. 20630 are very close to those in the type of *Claenodon procyonoides* from the New Mexico Torrejon. The isolated molar represents an individual slightly smaller. I was unable to find any characters of significance in these specimens by which the Bison basin form could be determined as distinct from the earlier *C. procyonoides*.

MEASUREMENTS IN MILLIMETERS OF LOWER TEETH IN SPECIMENS OF *Claenodon*, cf. *procyonoides* (MATTHEW), U.S.N.M. NO. 20630

Length of lower molar series, M_1 - M_3	24.0
M_1 , anteroposterior diameter : greatest transverse diameter.....	7.7:6.1
M_2 , anteroposterior diameter : greatest transverse diameter.....	8.0:6.7
M_3 , anteroposterior diameter : greatest transverse diameter.....	8.7:5.6

CLAENODON, cf. MONTANENSIS (Gidley), 1919

Plate 7, figure 4

A range in size of teeth indicated by about five claeodont specimens in the Bison basin suite includes the proportions of the type of *Claenodon montanensis* from the Torrejon stage of the Montana Fort Union. All these tentatively referred materials, as well as those of the smaller form discussed above, were derived from the vicinity of the saddle locality below the south rim of the Bison basin. There would appear to be no characters of significance in the rather fragmentary materials of this intermediate species which would serve to distinguish it from that of the earlier *C. montanensis*. Moreover, I suspect that additional material may render difficult its clear separation from that represented by the materials referred to *C. procyonoides*.

MEASUREMENTS IN MILLIMETERS OF TEETH IN SPECIMEN OF
Claenodon, cf. montanensis (GIDLEY), U.S.N.M. NO. 20574

M₂, anteroposterior diameter : greatest transverse diameter..... 9.5^a:7.5
M₃, anteroposterior diameter : greatest transverse diameter..... 9.8:6.3

^a Approximate.

CLAENODON, cf. FEROX (Cope), 1883

Plate 7, figures 2, 3

A somewhat larger series, including at least nine specimens, is most nearly comparable to the materials of *Claenodon ferox* that in the New Mexico collections were earlier distinguished as *Claenodon corrugatus*, or the lower portion of the size range for *C. ferox*. As well as jaw portions, there are in this group three fragmentary maxillae, each with two molars, and an isolated P³. In the portion of the histogram representing this material the three individuals indicated by dashed lines have M₃ preserved rather than M₂, and proportions of the latter are estimated by comparison with teeth in a better preserved individual of this group, U.S.N.M. No. 20633.

Whether or not the form represented by this group of specimens is the same as that tentatively referred to *C. montanensis*, there seems no certain evidence; nevertheless, the extremes in size when combined are strikingly far apart, and any attempt to group them together without rather conclusive evidence would seem an incompatible arrangement. Moreover, it should be particularly noted that although the actual size range of the individuals in such a lumped arrangement might be no more than in the *C. ferox* material of the Torrejon, the percentage of difference in the series is very much greater. For this

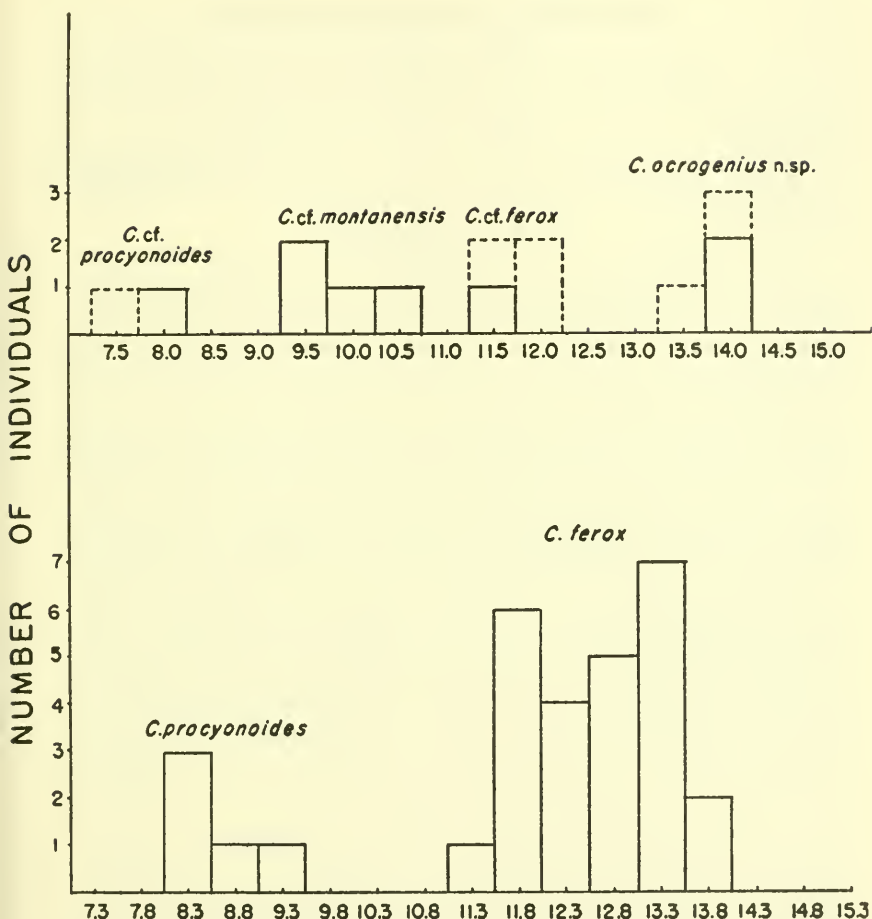


Fig. 2.—Histogram of length of M_2 of *Claenodon* from Bison basin Paleocene, above, and Torrejon (modified from Simpson, 1937) of New Mexico, below.

reason a histogram using a linearly arranged grouping of sizes is misleading unless this characteristic is understood.

MEASUREMENTS IN MILLIMETERS OF TEETH IN SPECIMENS OF
Claenodon, cf. *ferox* (COPE)

	U.S.N.M. No. 20797
M_2^* , anteroposterior diameter : transverse diameter*	10.7 : 15.9
M_3^* , anteroposterior diameter : transverse diameter	8.2 : 11.1
	U.S.N.M. No. 20633
M_2 , anteroposterior diameter : transverse diameter	11.4 : 10.4
M_3 , anteroposterior diameter : transverse diameter	12.7 : 9.1

* Transverse diameter taken lingually to base of enamel.

CLAENODON ACROGENIUS,¹¹ new species

Plate 7, figures 1, 6

Type.—Right ramus of mandible with P_1 , M_1 , and M_3 , U.S.N.M. No. 20634.

Horizon and locality.—Bison basin Tiffanian, saddle locality at south rim of Bison basin, sec. 28, T. 27 N., R. 95 W., Fremont County, Wyo.

Specific characters.—Size comparable to the very largest individuals of *Claenodon ferox*. Jaw very deep, particularly beneath position of anterior premolars. Canine large and anterior premolars separated by a marked diastema. P_2 possibly absent or reduced to single rooted tooth.

Discussion.—*Claenodon acrogenius* is represented by approximately seven specimens in the collections of the National Museum and possibly by a molar talonid in the University of Wyoming collection. Among the referred specimens are the posterior portions of three other lower jaws with one molar each, two maxillary fragments exhibiting M^1 , one of which also includes most of P^4 , and an isolated P_4 .

Although the size of the teeth in this material is within, or nearly within, the upper limits of the size range for *Claenodon ferox* as recognized in the Torrejon materials, the depth of the jaw, as shown in the type specimen, appears to be exceedingly great, particularly toward the forward extremity. Moreover, the type specimen has a large saberlike canine, as indicated by the root portion, and a diastema of very considerable length anterior to P_3 . P_1 is close to the canine and P_2 is missing. A short distance posterior to P_1 there is a depression that may have been an alveolus for a root of P_2 . It is uncertain, of course, but this tooth may have been lost during the life of the animal and the alveoli nearly obliterated. In any case, the length of the diastema between P_1 and P_3 is very much greater than would be required for a P_2 .

The two molars preserved in this jaw are much worn and do not include M_2 . These teeth are a little smaller than those in the other more fragmentary deep-jawed specimens and are interpreted as representing the smaller size group of *C. acrogenius* as shown in the histogram.

MEASUREMENTS IN MILLIMETERS OF TYPE OF *Claenodon acrogenius*,
U.S.N.M. NO. 20634

Length of cheek tooth series, posterior margin of alveolus of canine to posterior margin of M_3	87. ^a
Diastema between P_1 and P_3	15.0

¹¹ From Greek, *akrogeios* = with prominent chin.

Depth of jaw beneath diastema between P_1 and P_3	31.0
P_1 , anteroposterior diameter : transverse diameter	3.5 ^a : 2.2
P_3 , anteroposterior diameter at alveoli	11.0
P_4 , anteroposterior diameter at alveoli	13.5
M_1 , anteroposterior diameter : transverse diameter	12.2 : 9.7
M_3 , anteroposterior diameter : transverse diameter	15.0 ^e : 9.9

^a Approximate.^e Estimated.

MESONYCHIDAE

DISSACUS, sp.

Mesonychid creodont material is exceedingly scarce in the Bison basin collections, as only two incomplete teeth have been encountered. One of these is the outer portion of an upper cheek tooth, not identified as to position, but showing the high conical paracone, somewhat lower metacone, and a prominent parastyle characteristic principally of P_4 - M_2 in *Dissacus*. In size it is a trifle larger than M_2 in *D. navajovius* as illustrated by Matthew (1937, figs. 16, 17). The other specimen consists of about the posterior two-thirds of a lower cheek tooth. The anterior and medial portions of the protoconid, including the position of a possible metaconid, are missing. The shearing talonid is slightly longer than in the Torrejon *D. navajovius* tooth material in the National Museum collections. The material, however, is not adequate for specific diagnosis, although there would seem to be no doubt as to the genus represented.

MIACIDAE

DIDYMICTIS, near *D. TENUIS* Simpson, 1935

A lower jaw fragment with M_2 and the talonid of M_1 in the University of Wyoming collection (No. 1063) would appear to be the only determinable miacid material so far encountered in the Bison basin collecting. The specimen is from the vicinity of the saddle locality below the south rim of the basin. The species is clearly a minute form of *Didymictis* and the talonid of M_1 has proportions almost the same as in the type of *Didymictis tenuis* from the Gidley quarry in the Crazy Mountain Fort Union. M_2 is not preserved in the *D. tenuis* material, but the root portions shown in the type indicate a tooth slightly longer than that of the Bison basin specimen. However, this difference alone would not warrant recognition of a separate species. Nevertheless, it is probable, in view of the difference in age of the horizons represented, that the species are not the same. M_2 in No. 1063 measures 2.6 mm. long by 1.4 mm. wide. The talonid of M_1 is about 1.5 mm. wide.

CONDYLARTHRA HYOPSODONTIDAE

PROMIOCLAENUS PIPIRINGOSI,¹² new species

Plate 11, figures 1, 2

Type.—Right ramus of mandible with M_1 and M_2 , U.S.N.M. No. 20571.

Horizon and locality.—Bison basin Tiffanian, saddle locality at south rim of Bison basin, sec. 28, T. 27 N., R. 95 W., Fremont County, Wyo.

Specific characters.—Close in size of molar teeth to *Promioclænus lemuroides* (Matthew), but lower premolars noticeably smaller. Premolars simple and but slightly inflated. P_2 and P_3 without parastylid and without talonid cusps or crest. P_4 with only a vestige of a parastylid, no metaconid, but exhibiting two small cusps at posterior margin of a very short talonid. Molars relatively narrow transversely without entoconid, and hypoconulid on talonid rim of M_1 and M_2 well defined.

Discussion.—In addition to the type, a fragmentary jaw with P_2 - P_4 (U.S.N.M. No. 21021) and a maxilla with M^2 - M^3 (U.S.N.M. No. 21022) are believed to represent *Promioclænus pipiringosi*. The lower molars exhibited in the type are only slightly shorter anteroposteriorly than in the Torrejon *Promioclænus lemuroides* material at hand, but distinctly narrower relatively. Though worn, the cusps on the marginal crest of the talonid appear comparatively well defined, rather more as in teeth of the distinctly smaller *Promioclænus aquilonius* of the Montana Fort Union. The lower premolars, if No. 21021 is correctly referred, are small and not so inflated as in *P. lemuroides*, though less slender than in *P. aquilonius*. Moreover, the anterior premolars are without parastylid or any talonid cusps. P_4 , however, shows a slight parastylid and a pair of cusps on the talonid; nevertheless, there is no evidence of a metaconid so generally observed on this tooth in *P. aquilonius*. The two upper molars in the tentatively referred maxillary fragment are much worn and exhibit few characters of significance. The individual represented is a little smaller than the type. The external cingulum is prominent between the paracone and metacone and divided about midway.

Use of the generic designation *Promioclænus* Trouessart, rather than *Ellipsodon*, for these forms, is in conformity with Dr. R. W. Wilson's findings (1952) with respect to the genotype *Ellipsodon inaequidens*. Trouessart proposed *Promioclænus* for the two species

¹² Named for George N. Pipiringos, of the U. S. Geological Survey.

P. acolytus and *P. lemuroides*. Presumably *P. acolytus* (Cope), the first of the two listed by Trouessart, is to be regarded as the genotype.

MEASUREMENTS IN MILLIMETERS OF TEETH IN SPECIMENS OF

Promioclænus pipiringosi

	U.S.N.M. No. 21021
P ₂ , anteroposterior diameter : greatest transverse diameter.....	2.7 : 1.6
P ₃ , anteroposterior diameter : greatest transverse diameter.....	3.3 : 2.1
P ₄ , anteroposterior diameter : greatest transverse diameter.....	3.8 : 2.8

	U.S.N.M. No. 20571 (type)
M ₁ , anteroposterior diameter : greatest transverse diameter.....	4.1 : 3.4
M ₂ , anteroposterior diameter : greatest transverse diameter.....	4.4 : 3.7

PROMIOCLAENUS? sp.

A very large species of *Promioclænus* may be represented by a fragmentary right mandibular ramus (U.S.N.M. No. 21020), having preserved only the posterior portion of M₂ and part of the trigonid as well as the roots of M₃. The form is close in size to *Litaletes disjunctus* Simpson of the Montana Fort Union. M₃ would appear to be fully as large as in *L. disjunctus*, a relative size quite unlike typical *Ellipsodon*. There is a distinct possibility that this is *Litaletes* rather than *Promioclænus*; however, the cusps included in the preserved portion of M₂, though somewhat worn, suggest a lower crowned tooth as in *Promioclænus*, distinctly less inflated than in *Mioclænus*.

LITOMYLUS SCAPHICUS,¹³ new species

Plate 8, figures 2, 4

Type.—Right ramus of mandible with M₂ and M₃, U.S.N.M. No. 21014.

Horizon and locality.—Bison basin Tiffanian, saddle locality at south rim of Bison basin, sec. 28, T. 27 N., R. 95 W., Fremont County, Wyo.

Specific characters.—Lower molars larger and relatively wider than in *Litomylus dissentaneus*. Cusps relatively lower and more inflated, with paraconid more reduced.

Discussion.—There would seem no doubt but that the genus *Litomylus*, originally described by Simpson on the basis of the species *L. dissentaneus* in the Torrejonian of the Montana Fort Union, is represented by two distinct species in the Bison basin Tiffanian. *Litomylus*

¹³ *Skaphikos*, from Greek *skaphos* = anything hollowed out as a basin, in allusion to the Bison basin.

scaphicus, the larger, is represented at the saddle locality by the type specimen, and at the ledge locality, about one-quarter mile to the west, by a second jaw portion, U.S.N.M. No. 21015, almost identical to it.

An upper molar, U.S.N.M. No. 21013, possibly M^1 , from the saddle locality is structurally very much like the first or second upper molars in *L. dissentaneus*, except that the protoconule and metaconule are less well defined.

Measurements of the teeth of this form are included with those of the following species.

LITOMYLUS SCAPHISCUS,¹⁴ new species

Plate 8, figure 5

Type.—Right ramus of mandible with P_3 , M_1 and M_2 , U.S.N.M. No. 21010.

Horizon and locality.—Bison basin Tiffanian, ledge locality at south rim of Bison basin, $W\frac{1}{2}$ sec. 28, T. 27 N., R. 95 W., Fremont County, Wyo.

Specific characters.—Size of teeth close to those in *Litomytus dissentaneus*, distinctly less than in *L. scaphicus*, P_3 with parastylid and posterior cusps much better developed than in *L. dissentaneus*. Paraconid on molars more reduced. Talonid basin a little less deeply pocketed.

Discussion.—A second jaw fragment with M_1 and part of M_2 , U.S.N.M. No. 21011, is also from the ledge locality and a single lower molar of this small species was encountered at the saddle but no material was obtained from the west end of the basin.

Litomytus scaphiscus resembles the larger *L. scaphicus* in the more reduced paraconids of the lower molars but is strikingly close in size of both premolars and molars to *L. dissentaneus*. It differs from *L. dissentaneus* essentially in the better development of the cusps of P_3 , the weaker paraconids of the molars (particularly M_1), and the less deeply basined molar talonids. Moreover, the depth of the pocket is greatest nearer the lingual margin than in *L. dissentaneus*.

MEASUREMENTS IN MILLIMETERS OF TEETH IN TYPE SPECIMENS OF TWO NEW SPECIES OF *Litomytus*

	<i>L. scaphiscus</i> U.S.N.M. No. 21014 (type)	<i>L. scaphiscus</i> U.S.N.M. No. 21010 (type)
P_3 , anteroposterior diameter : greatest transverse diameter		3.7 : 1.65
P_4 , anteroposterior diameter : greatest transverse diameter		3.8° : —

¹⁴ *Skaphiskos*, from Greek *skaphos* (diminutive form) = hollowed out as a basin, in allusion to the Bison basin.

M ₁ , anteroposterior diameter : greatest transverse diameter	3.2 : 2.2
M ₂ , anteroposterior diameter : greatest transverse diameter	3.6 : 3.1
M ₃ , anteroposterior diameter : greatest transverse diameter	3.3 : 2.5
M ₃ , anteroposterior diameter : greatest transverse diameter	3.8 : 2.6

* Estimated.

HAPLALETES PELICATUS,¹⁵ new species

Plate 9, figure 1

Type.—Left ramus of mandible with P₃-M₃, U.S.N.M. No. 21008.

Horizon and locality.—Bison basin Tiffanian, saddle locality at south rim of Bison basin, sec. 28, T. 27 N., R., 95 W., Fremont County, Wyo.

Specific characters.—Length of lower molar series about one-fifth greater than that of *Haplaletes disceptatrix*. Premolars more inflated. Metaconid of P₄ weaker. Paraconid weak on M₁, vestigial or absent on M₂ and M₃. External cingulum weak and discontinuous or absent on lower molars.

Discussion.—The type of *Haplaletes pelicatus* is an excellent lower jaw with the cheek-tooth series in a nearly unworn state. Among the referred materials are three lower-jaw fragments each with one molar, all from the same locality as the type. Two of the latter are in the collections of the University of Wyoming.

The teeth in U.S.N.M. No. 21008 bear a striking resemblance to those in the type of *H. disceptatrix* from the earlier or Torrejonian equivalent of the Fort Union, particularly in the form and slope of the molar cusps. The premolars, however, are a little more inflated and as a consequence the metaconid of P₄ is not so prominent. *Haplaletes* is rather distinctive among condylarths, and the posterior molars, particularly M₃, look surprisingly like these teeth in *Thryptacodon*. The first molars, however, bear little resemblance.

Comparison of *Haplaletes pelicatus* with *Haplaletes diminutivus* Dorr (1952) is not feasible inasmuch as the latter is represented by a partial upper dentition; nevertheless the very small size of the Dell Creek form leaves no doubt as to their distinctness.

Measurements of teeth in *H. pelicatus* are included with those of the following species.

HAPLALETES SERIOR,¹⁶ new species

Plate 9, figure 2

Type.—Left ramus of mandible with M₂ and M₃, U. of Wyo. No. 1078.

¹⁵ From Greek, *pelike* = basin, in allusion to the Bison basin.

¹⁶ *Serior* = later, with reference to its stratigraphic position.

Horizon and locality.—Bison basin Tiffanian, *Titanoides* locality, southwestern portion of basin, sec. 29, T. 27 N., R. 95 W., Fremont County, Wyo.

Specific characters.—Lower molar teeth about 15 percent longer and nearly 22 percent wider transversely than in *Haplaletes pelicatus*. Paraconid on M_2 and M_3 vestigial. Talonid basin shallow. Hypoconulid of M_3 broader and less protruding posteriorly. No external cingulum.

Discussion.—The type of *Haplaletes serior* is the only known specimen and comes from near where the *Titanoides* upper teeth were discovered, about a mile west of the saddle locality, and apparently a little higher stratigraphically.

Haplaletes serior is a larger form than *H. pelicatus* with relatively wider molars. The form appears, from the limited material, to represent the same genus as *H. pelicatus* but would seem more distinct from *H. disceptatrix*. However, the difference from the latter is for the most part a rather marked disparity in size.

MEASUREMENTS IN MILLIMETERS OF TEETH IN TYPE SPECIMENS OF
TWO NEW SPECIES OF *Haplaletes*

	<i>H. pelicatus</i> U.S.N.M. No. 21008 (type)	<i>H. serior</i> U. of Wyo. No. 1078 (type)
P_3 , anteroposterior diameter : greatest transverse diameter	2.6 ^a : 1.6 ^a
P_4 , anteroposterior diameter : greatest transverse diameter	3.3 : 2.0
M_1 , anteroposterior diameter : greatest transverse diameter	3.0 : 2.3
M_2 , anteroposterior diameter : greatest transverse diameter	3.2 : 2.8	3.7 : 3.4
M_3 , anteroposterior diameter : greatest transverse diameter	3.3 : 2.6	3.7 : 3.1

^a Approximate.

PROTOSELENE? NOVISSIMUS,¹⁷ new species

Plate 8, figures 1, 3

Type.—Left ramus of mandible with M_2 and M_3 , U.S.N.M. No. 20572.

Horizon and locality.—Bison basin Tiffanian, saddle locality at south rim of Bison basin, sec. 28, T. 27 N., R. 95 W., Fremont County, Wyo.

¹⁷ *Novissimus* = youngest or latest, with reference to the stratigraphic horizons for *Protoselene*.

Specific characters.—Lower molars a little smaller and relatively more slender than in *Protoselene opisthacus*. Paraconid on M_2 and M_3 slightly lingual to midposition and distinctly isolated from both protoconid and metaconid. Talonid crest, particularly the crista obliqua, lower, and basin a little shallower.

Discussion.—A single M_1 (U.S.N.M. No. 21023) is known in addition to the type and was found at the same locality.

Protoselene? novissimus may not represent this genus but is much closer to it than to any other known condylarth. It has elongate molars approximating the selenodonty exhibited in *P. opisthacus*, but the crests are lower and consequently the basins a little more shallow appearing. The paraconid is located in about the same position, but on the posterior molars is more definitely isolated from the adjacent cusps. The extent to which this cusp is joined by a crest to the protoconid, however, is variable in the Torrejon form. M_2 in the type specimen measures 5.4 mm. long by 3.8 mm. wide. M_3 is 5.5 by 3.2 mm.

The isolated M_1 can be nearly matched in material of *P. opisthacus* but in each case the trigonid and talonid basins are a little shallower and the crista obliqua between the hypoconid and trigonid is a little more depressed. M_1 measures 5.6 mm. long by 3.6 mm. wide.

LITOLESTES LACUNATUS,¹⁸ new species

Plate II, figures 3, 4

Type.—Left ramus of mandible with P_4 and M_1 , U.S.N.M. No. 21016.

Horizon and locality.—Bison basin Tiffanian, *Titanoides* locality, southwestern portion of Bison basin, sec. 29, T. 27 N., R. 95 W., Fremont County, Wyo.

Specific characters.—Approximately a third larger than *Litolestes notissimus* in size of lower molars and well outside the range given by Simpson (1937a). Lower premolars relatively larger. P_4 with small anterolingual parastylid, metaconid weak and close to primary cusp, and two small talonid cuspules very close together. Paraconid weak or absent on M_2 and M_3 . Metaconid and protoconid about equal on M_1 and M_2 , and metaconid higher on M_3 . Entoconid comparatively high on all three molars.

Discussion.—The form herein described as *Litolestes lacunatus* is the smallest of the condylarths recognized in the Bison basin collections, yet it is distinctly larger than either of the previously described

¹⁸ *Lacunatus* = hollowed out, with reference to the Bison basin.

species of this Tiffanian genus. The genotype *Litolestes ignotus* Jensen is from the Silver Coulee horizon in the Polecat Bench series and *L. notissimus* from the Melville portion of the Crazy Mountain Fort Union. *Litolestes lacunatus* is represented in the Bison basin collections by two additional specimens from the same locality as the type: a lower jaw fragment with M_1 and M_2 (U. of Wyo. No. 1083) and a jaw fragment with M_3 and part of M_2 (U. of Wyo. No. 1079). A lower jaw portion with P_3 , P_4 , and a much worn M_1 (U. of Wyo. No. 1059) from the saddle locality may represent this species, but P_4 is lower and wider and lacks any evidence of a metaconid; moreover, the details of M_1 are rather obscured by wear. A jaw fragment with only P_4 (U.S.N.M. No. 21017) corresponds very closely to the type but came from the locality at the extreme west end of the basin.

A maxilla (U.S.N.M. No. 20931) from the west-end locality exhibiting P^3 - M^2 has rather well worn molars; nevertheless there seems no doubt that it represents *Litolestes lacunatus*. P^3 and P^4 are nearly similar to those teeth in *L. notissimus*, but the parastyle, a very small cusp on P^3 in *L. notissimus*, is absent on this tooth in *L. lacunatus*, however, that on P^4 is more robust in *L. lacunatus*. The parastyle and perhaps the metastyle on the molars are not so outstanding buccally as in *L. notissimus*. Moreover, the talon portions of the molars appear to be a little broader anteroposteriorly in the Bison basin specimen.

MEASUREMENTS IN MILLIMETERS OF TEETH IN SPECIMENS OF
Litolestes lacunatus

	U.S.N.M. No. 21016 (type)
P_4 , anteroposterior diameter : greatest transverse diameter.....	3.2 : 1.9
M_1 , anteroposterior diameter : greatest transverse diameter.....	2.7 : 2.0
	U. of Wyo. No. 1079
M_3 , transverse diameter of talonid.....	2.2
M_3 , anteroposterior diameter : greatest transverse diameter.....	2.2 : 1.6

PHENACODONTIDAE

GIDLEYINA WYOMINGENSIS, new species

Plate 9, figures 3, 4

Type.—Right ramus of mandible with P_3 - M_1 , U.S.N.M. No. 20790.

Horizon and locality.—Bison basin Tiffanian, locality at west end of Bison basin, $N\frac{1}{2}$ sec. 29, T. 27 N., R. 95 W., Fremont County, Wyo.

Specific characters.—Size of P_4 and molars close to that in *Gidleyina silberlingi*. P_3 much smaller and with simple posterior median crest and single talonid cusp. Paraconid of lower molars variable but generally low and weak. Trigonid not so prominently basined as in *Gidleyina superior*. Upper molars with prominent styles, and crests of protocone distinctive.

Discussion.—*Gidleyina wyomingensis* is better represented in the more westerly and stratigraphically somewhat higher levels than at the saddle locality. The type is from the locality at the west end of the basin, as are about eight other specimens, although most of these are isolated upper and lower teeth. The material from the ledge locality seems entirely similar to that from the west-end locality, and among the 10 specimens from the ledge is the upper dentition (U.S.N.M. No. 20795) figured in plate 9 and about three jaws with two or more molars. About five specimens from the saddle locality, including portions of upper and lower dentitions, might well represent a slightly smaller variant, though probably not specifically distinct from that represented in the material from the more westerly collecting sites.

Doubt may be logically entertained as to the advisability of recognizing *Gidleyina* as distinct from *Ectocion*. Comparison of the Tiffanian materials with the genotype of *Ectocion*, *E. osbornianum*, from the lower Eocene would seem to justify separate recognition but, as may be expected, the Clarkforkian materials, particularly those from the Almy, in no way simplify this arrangement. As noted by Simpson, the upper premolars in *Gidleyina* are less progressive and the upper molars show better development of crests from the protocone to the protoconule and metaconule. No upper premolars appear to be included in the Bison basin collections but the molars exhibit the protocone crests as mentioned above, and in comparison with *G. montanensis* have perhaps somewhat better developed external styles. P_4 in both the Montana and Wyoming *Gidleyina* material would appear distinctive when compared with Eocene material of *Ectocion*, principally in that the trigonid is elongate in comparison with the talonid length, whereas in *E. osbornianum* this relationship is rather generally reversed with the trigonid often short and broad and the talonid usually, though not invariably, better developed. Moreover, in some individuals of *E. osbornianum* the talonid of P_4 looks quite molariform, with a surprisingly well developed entoconid.

With regard to the forms of *Gidleyina* known from the Melville unit of the Montana Fort Union, I strongly suspect that *Gidleyina silberlingi* is a synonym of *G. montanensis*. Simpson (1937b) called

attention to this possibility at the time he published Gidley's descriptions. There is some difference in the stratigraphic levels attributed to the two, but not as much difference as between either of them and *Gidleyina superior*. Nevertheless, to judge by the variation in molar structure noted for both *Gidleyina* and *Ectocion*, *G. superior* may be no more than a variant of *G. montanensis*. The possibility also remains that *G. wyomingensis* is likewise not distinct, but possible synonymy here awaits demonstration that the lower premolars exhibited in the type of *G. silberlingi* are atypical.

A form which Simpson (1935c) described as *Phenacodus gidleyi* in the Tiffany fauna has teeth only a trifle larger than in *G. wyomingensis*, but the trigonid portions of the lower teeth in the type of *P. gidleyi* represent a little greater proportion of the tooth length than in *G. wyomingensis*. I am unable to determine whether *P. gidleyi* represents *Phenacodus* or *Gidleyina*.

MEASUREMENTS IN MILLIMETERS OF TEETH IN SPECIMENS OF
Gidleyina wyomingensis

	U.S.N.M. No. 20795	
Length of upper molar series, M ¹ -M ³	20.1	
M ¹ , anteroposterior diameter : greatest transverse diameter.....	7.4 : 9.6 ^a	
M ² , anteroposterior diameter : greatest transverse diameter.....	7.2 : 10.4	
M ³ , anteroposterior diameter : greatest transverse diameter.....	5.7 : 8.4	
	U.S.N.M. No. 20790 (type)	U.S.N.M. No. 20793
P ₃ , anteroposterior diameter : greatest transverse diameter	5.8 : 3.5
P ₄ , anteroposterior diameter : greatest transverse diameter	6.8 : 4.7
M ₁ , anteroposterior diameter : greatest transverse diameter	6.5 : 5.2	6.6 : 5.2
M ₂ , anteroposterior diameter : greatest transverse diameter	6.8 : 5.6
M ₃ , transverse diameter of trigonid.....	4.8

^a Approximate.

PHENACODUS? BISONENSIS,¹⁹ new species

Plate 10, figures 1-3

Type.—Right maxilla with P⁴-M², U.S.N.M. No. 20564, and probably a left maxilla with M¹ and M² believed to be from the same individual.

Horizon and locality.—Bison basin Tiffanian, vicinity of saddle locality at south rim of Bison basin, sec. 28, T. 27 N., R. 95 W., Fremont County, Wyo.

¹⁹ Named for the Bison basin.

Specific characters.—Size very close to that of *Phenacodus almiensis*, about intermediate between that of *Phenacodus? grangeri* and *Phenacodus? matthewi* of the Tiffany beds. P^3 and P^4 with tritocone distinct, but much less progressive than in *P. almiensis*. Mesostyle prominent on M^1 but variable on M^2 . Lower premolars comparatively simple and unprogressive. P^4 trigonid with paraconid low and forward, and talonid weakly basined, with entoconid generally distinct though small.

Discussion.—Approximately 30 specimens of this form are at hand and nearly all are from the vicinity of the saddle locality. Two specimens, however, were secured from the ledge locality stratigraphically a little higher.

Uncertainty exists as to whether the species represented by this material should be referred to *Phenacodus* or to *Tetraclaenodon*. Its allocation to *Phenacodus* is entirely arbitrary and scarcely more than an impression. As noted by Granger (1915), there are actually no clear-cut characters by which the genera may be separated. Although there are differences between them in degree of development for a number of characters, they are in the nature of average differences, lacking in the consistency generally expected at the generic level. Granger attempted a definition based on the development of the mesostyle, but certain upper molars of *Tetraclaenodon puercensis* show a rather surprising prominence in this style. The shift of the metaconule posteriorward would seem evident for *Phenacodus primaevus* but not diagnostic for such Paleocene forms as *Phenacodus almiensis* or *Phenacodus? grangeri*. I note a decreasing prominence of the protoconule and metaconule with respect to the primary cusps in rising above the Torrejon level, to the extent that in some Wasatchian material of *Phenacodus* the metaconule is entirely missing on M^2 and M^3 . Nevertheless, this is variable in populations of the better known species of *Phenacodus* as well as in *Tetraclaenodon puercensis*, and, like the increasing significance of the tritocone of the upper premolars, is a difference in degree not readily defined.

The lower teeth do not appear to present characters of significance on a generic level. Certainly the development or reduction of the paraconid is too highly variable. The talonid of P_4 would seem to become more molariform in time and the entoconid better developed but this cusp is occasionally prominent in material of *Tetraclaenodon puercensis*, and a decidedly primitive appearing P_4 structure has been observed in material representing certain of the smaller species of *Phenacodus* in the Eocene.

Phenacodus? bisonensis would appear to be *Tetraclaenodon* in the subordinate appearance of the tritocone on P^3 and P^4 and its proximity

to the primary cusp, and in this respect is certainly distinct on a specific level from the Clarkforkian materials, such as *Phenacodus almiensis*. Nevertheless, these teeth show deuterocone portions more suggestive of *Phenacodus*, and P^3 has a rather conspicuously developed postero-internal talon basin not observed in U. S. National Museum Torrejon materials. *P.?* *bisonensis*, moreover, resembles *P. almiensis* in the slightly more crested appearance of the upper molar cusps and in the lesser significance of the conules in comparison with *Tetraclaenodon puericensis*. The mesostyle of the upper molars is distinct and moderately prominent in all referred materials; however, in the type specimen, although prominent on M^1 , it is very weak on M^2 .

MEASUREMENTS IN MILLIMETERS OF TEETH IN SPECIMENS OF
Phenacodus? bisonensis

	U.S.N.M. No. 20566	U.S.N.M. No. 20564 (type)
P^3 , anteroposterior diameter : transverse diameter ...	7.8:6.5
P^4 , anteroposterior diameter : transverse diameter ...	7.2:8.0	8.3: 9.2
M^1 , anteroposterior diameter : greatest transverse diameter	9.4: 11.0
M^2 , anteroposterior diameter : greatest transverse diameter	9.4: 12.8
	U.S.N.M. No. 20567	U.S.N.M. No. 20569
Length of lower molar series.....	28.7
P_3 , anteroposterior diameter : greatest transverse diameter	7.7:4.6
P_4 , anteroposterior diameter : greatest transverse diameter	8.8:5.7
M_1 , anteroposterior diameter : greatest transverse diameter	8.9:7.6	8.2:7.3
M_2 , anteroposterior diameter : greatest transverse diameter	9.5 ^a :7.4	9.6:8.2
M_3 , anteroposterior diameter : greatest transverse diameter	10.5:7.2

^a Approximate.

PHENACODUS? sp. (large)

Plate 10, figures 4, 5

A fragmentary right mandibular ramus with M_3 , U.S.N.M. No. 21025, an isolated P^3 , M^3 , and an incomplete lower molar (the latter two in the collections of the University of Wyoming) are of a species much larger than *Phenacodus? bisonensis*. The range of size represented in materials of *P.?* *bisonensis* is surprisingly limited, certainly in comparison with such forms as *T. puericensis* and *P. primae-vus*, so that the teeth here indicated as of a distinct species stand out

conspicuously in the collections. The form represented may be *Phenacodus? grangeri* which Simpson (1935c) described from the Colorado Tiffany, but the measurements where equivalent materials are present noticeably exceed those of the more southern animal. M_3 which measures 13.6 by 9.2 mm., for example, is 19 percent longer and 12 percent wider. This difference in a form such as *Phenacodus* might not be important. The significance would, of course, depend on the position of these two examples with regard to their respective but unknown means.

The third lower molar apparently reveals no information as to whether references should be made to *Phenacodus* or *Tetraclaenodon*. P^3 , however, as in *P.? bisonensis* has a well-developed posterointernal basin and the tritocone is apparently better defined than usual in *Tetraclaenodon puercensis*. The isolated M^3 has a distinct but small mesostyle and the hypocone is particularly small.

PANTODONTA

CORYPHODONTIDAE

TITANOIDES PRIMAEVUS Gidley, 1917

Plate 11, figure 5

The finding in North Dakota by a party under the direction of Dr. Glenn L. Jepsen of portions of the skull including the upper dentition belonging beyond doubt to the type of *Titanoides primaevus* was unusually good fortune, so that no uncertainty now exists as to the characteristics of the superior dentition of this upper Paleocene pantodont. Patterson early (1933) described new materials from the Platteau Valley beds of Colorado as representing *Titanoides*, but upon later discovery of at least three pantodont forms from these beds, with distinguishing features in the upper dentition, was forced to regard all as distinct from *Titanoides* and the species at first referred to *Titanoides* was given the new generic name *Barylambda*. It now develops, with the finding of *Titanoides* upper teeth, that while *Barylambda* and *Haplolambda* are clearly distinct, *Sparactolambda*²⁰ is the form which I believe must now be regarded as the synonym of *Titanoides*.

In the University of Wyoming material from the Bison basin there

²⁰ Jepsen's discovery has likewise permitted us to determine correctly the identity of an excellent pantodont skull collected by Dr. T. E. White in McKenzie County, N. Dak., and, like the type of *T. primaevus*, from the general area of the type Fort Union. This skull, originally and with apparent correctness, determined by White as representing *Sparactolambda*, is now seen to belong beyond doubt to *Titanoides primaevus*.

is a right maxilla (U. of Wyo. No. 1093) with three little-worn upper molars. The resemblance of these teeth to those in the type of *Titanoides primaevus* is striking so that no doubt exists as to the identity. The teeth in No. 1093 are slightly smaller in all dimensions, except M^3 , and are nearly similar in form. Observable differences include a better developed metacone on the molars, and M^3 shows, in addition to a slightly larger size, the parastyle directed somewhat more laterally in No. 1093, not so forward as in the type. Very slight differences noted are a less developed protoconule on M^2 and metaconule on M^3 .

MEASUREMENTS IN MILLIMETERS OF UPPER MOLARS IN SPECIMEN OF

Titanoides primaevus GIDLEY, U. OF WYO. NO. 1093

Length of upper molar series, M^1 - M^3	66.8
M_1 , anteroposterior diameter : transverse diameter *	20.8 : 23.3
M_2 , anteroposterior diameter : transverse diameter *	25.3 : 27.9
M_3 , anteroposterior diameter : greatest transverse diameter.....	20.4 : 34.0

* Anteroposterior diameters of M_1 and M_2 taken across outer styles and transverse diameters perpendicular to line between outer styles. Anteroposterior diameter of M_3 taken perpendicular to anterior face.

CAENOLAMBDA,²¹ new genus

Type.—*Caenolambda pattersoni*, new species.

Generic characters.—Skull with elongate cranium, strong, arched sagittal crest, broad frontals, narrow nasals and heavy canines resembling the *Titanoides* group. Upper cheek teeth, though comparatively small, are anteroposteriorly shortened and transversely broad as in the *Barylambda*-*Haplolambda* group, but with molars M^1 to M^3 about equaling one another in size.

Discussion.—*Caenolambda* presents a rather unusual combination of characters and does not closely resemble any of the previously described genera. Nevertheless, in a general way, the skull is apparently more like *Titanoides* than *Barylambda* or *Haplolambda*. This is noticed in the relatively elongate cranium and strong, arched sagittal crest. It resembles the cast of the paratype of "*Sparactolambda*" *looki* in narrowness of the nasals, although the nasal cavity is apparently not so large. As in the latter and the type of *Titanoides primaevus* the canine is very well developed. The upper cheek teeth, however, are decidedly different. The teeth are distinctly shortened anteroposteriorly, particularly the lingual portions, and very broad transversely. The external styles at the anterior and posterior angles of the teeth do not project laterally to such an extent and the primary external cusps are somewhat closer to the labial margin of the tooth, so that

²¹ From Greek *kainos*, recent or new, + *lambda*, the Greek letter—named in analogy with *Pantolambda*, *Barylambda*, *Archaeolambda*, and others.

the characteristic "V" and "W" shapes to the outer cusps are not so transversely extended as in *Titanoides*, or the more extreme condition seen in *Archaeolambda*. The relatively great width is composed largely of the talon, and in the molars, as clearly shown in M^2 , there is a strong ledgelike cingulum about the lingual and posterior margin. On *Titanoides* molars the lingual cingulum is weak, although better developed along the posterior margin of the premolars than in *Caenolambda*. The molars of *Caenolambda* would appear to be about equal to one another in size as in *Pantolambda*, not showing the marked increase from M^1 to M^3 seen in *Titanoides*, or the reduction of M^3 noted in *Barylamba* and *Haplolambda*.

The skull of *Barylamba* is large and relatively broader than that of *Caenolambda*. The nasal cavity is larger and the nasal bones much wider. The frontals are broad in both forms, but *Barylamba* does not exhibit a sagittal crest so heavy and prominently arched as in *Caenolambda*. The teeth of *Barylamba* are transversely broad in comparison to their anteroposterior dimension, as in *Caenolambda*, but the talon of molars, particularly M^1 and M^2 , is not nearly so slender; moreover, the cingulum is weak or absent lingually rather than shelf-like. M^3 , as noted above, is much reduced in *Barylamba*.

The comparisons between *Haplolambda* and *Caenolambda* are rather similar to those between *Barylamba* and *Caenolambda*, although the species *Haplolambda quinmi* and *Caenolambda pattersoni* are more nearly comparable in size. The cranial portion of *Haplolambda* is shorter and the sagittal crest not so arched as in *Caenolambda*, but the nasals are wider and the nasal cavity larger although the frontals are not so broad. The cheek teeth resemble those of *Caenolambda* in their relative width and the distinctly labial position of the primary external cusps, but again as in *Barylamba* the molar talons are not so slender, the cingulum is lingually weak, and M^3 is reduced. In *Haplolambda*, moreover, M^1 would appear to be larger than M^2 , quite the reverse of *Titanoides*. The comparatively small canine in *Haplolambda* would appear to be a striking difference from both *Caenolambda* and *Titanoides*, but the size of this tooth is so often a matter of dimorphism that one hesitates to stress the character. Nevertheless, if there is any dimorphism in this respect within species of *Coryphodon*, it is certainly much less evident.

CAENOLAMBDA PATTERSONI,²² new species

Plates 12-14

Type.—Skull, lacking zygomatic arches and mandible, U.S.N.M. 21036.

²² Named for Bryan Patterson in appreciation of his work on the pantodonts.

Horizon and locality.—Bison basin Tiffanian, vicinity of saddle locality at south rim of Bison basin, sec. 28, T. 27 N., R. 95 W., Fremont, Wyo.

Specific characters.—Length of skull greater than that of *Haplo-lambda quinni* but less than *Titanoides primaevus*. Much smaller than *Barylambda faberi*. Cheek teeth comparatively small. Other characters not distinguished from those discussed above as characterizing the genus.

Discussion.—Except for a few isolated teeth or tooth fragments which may represent this species, there are no determinable materials other than the type. Moreover, the more fragmentary specimens cannot be allocated as between this form and *Titanoides primaevus*, the latter having been certainly encountered only at the *Titanoides* locality, at a level believed to be higher stratigraphically than the saddle.

The skull designated the type of *Caenolambda pattersoni* is advanced in maturity so that the teeth are rather well worn, with the characters of M^1 almost obliterated. Moreover, the sutures are nearly all obscured so that little is revealed of the surface extent of the separate elements of the skull. This situation was further complicated by the fact that the skull was discovered in a dense limestone nodule and during its preparation much difficulty was experienced determining the actual boundary between bone and matrix. As a result much in the way of important detail cannot be discerned.

MEASUREMENTS* IN MILLIMETERS OF SKULL, U.S.N.M. NO. 21036,
TYPE SPECIMEN OF *Caenolambda pattersoni*

Length of skull from the anterior margin of premaxillae to posterior margin of occipital condyles.....	320.
Length from anterior margin of canine alveolus to posterior margin of occipital condyles.....	300.
Distance from posterior margin of palate at posterior narial aperture to posterior margin of occipital condyles.....	170.
Width across postorbital processes.....	110.
Width across nasals about midway of length.....	24.
Length of upper dentition, C (at alveolus) to M^3 , incl.....	135.
Length of upper cheek tooth series, P^3 to M^3 , incl.....	92.
Length of upper molar series, M^1 to M^3	52.
C, anteroposterior diameter (at alveolus) : greatest transverse diameter	26.0 : 16.0
P^2 , anteroposterior diameter : transverse diameter	13.0 : 19.0
P^3 , anteroposterior diameter : transverse diameter	13.0 : 23.0
P^4 , anteroposterior diameter : transverse diameter	13.5 : 23.5
M^1 , anteroposterior diameter : transverse diameter	18.5 : 27.0
M^2 , anteroposterior diameter : transverse diameter	19.0 : 30.0
M^3 , anteroposterior diameter : transverse diameter	16.0 : —

* Measurements are nearly all approximate owing to fracturing and distortion of skull, and teeth are much worn and nearly all slightly damaged at styles. Tooth measurements include styles and are taken parallel to and at right angles to direction of tooth row.

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EXPLANATION OF PLATES

PLATE I

MULTITUBERCULATES AND INSECTIVORES FROM THE BISON BASIN PALEOCENE

- Fig. 1. Cf. *Ptilodus montanus* Douglass: Left P₄ (U.S.N.M. No. 20877), lateral view. Four times natural size.
- Fig. 2. Cf. *Ectypodus hazeni* Jepsen: Left P₄ (U.S.N.M. No. 20878), lateral view. Four times natural size.
- Fig. 3. Cf. *Ectypodus musculus* Matthew and Granger: Left ramus of mandible with M₁ (U. of Wyo. No. 1105), occlusal view. Four times natural size.
- Fig. 4. Cf. *Anconodon russelli* (Simpson): Right ramus of mandible with P₄ (U. of Wyo. No. 1065), lateral view. Four times natural size.
- Fig. 5. *Bisonalveus browni*, new genus and species: Left ramus of mandible (U.S.N.M. No. 20928), type specimen, lingual and occlusal views. Four times natural size.
- Fig. 6. *Diacondon pearcei*, new species: Left ramus of mandible (U.S.N.M. No. 20970), type specimen, lingual and occlusal views. Four times natural size.

PLATE 2

PRIMATES AND MARSUPIALS FROM THE BISON BASIN PALEOCENE

- Figs. 1, 2. *Pronothodectes*, cf. *matthewi* Gidley: 1, Left ramus of mandible (U.S.N.M. No. 20758), lateral and occlusal views; 2, right ramus of mandible (U. of Wyo. No. 1062), lateral and occlusal views. Three times natural size.
- Fig. 3. *Plesiadapis*, cf. *fodinatus* Jepsen: Left ramus of mandible (U.S.N.M. No. 20784), lateral and occlusal views. Three times natural size.
- Figs. 4, 5. *Peradectes pauli*, new species: 4, Left ramus of mandible (U.S.N.M. No. 20879), type specimen, lingual and occlusal views; 5, left ramus of mandible (U.S.N.M. No. 20880), lingual and occlusal views. Four times natural size.
- Fig. 6. *Peradectes elegans* Matthew and Granger: Right ramus of mandible (U. of Wyo. No. 1104), lingual and occlusal views. Four times natural size.

PLATE 3

PRONOTHOECTES FROM THE BISON BASIN PALEOCENE

- Figs. 1, 3. *Pronothodectes simpsoni*, new species: 1, Right ramus of mandible (U.S.N.M. No. 20754), type specimen, lateral and occlusal views; 3, right ramus of mandible (U.S.N.M. No. 20770), lateral and occlusal views. Three times natural size.
- Fig. 2. *Pronothodectes*, cf. *simpsoni*, new species: Left ramus of mandible (U. of Wyo. No. 1057), lateral and occlusal views. Three times natural size.

PLATE 4

PLESIADAPIS FROM THE BISON BASIN PALEOCENE

Figs. 1-3. *Plesiadapis jepsoni*, new species: 1, Left ramus of mandible (U.S.N.M. No. 20586), lateral and occlusal views; 2, left maxilla (U.S.N.M. No. 20781), occlusal view; 3, left ramus of mandible (U.S.N.M. No. 20760), type specimen, lateral and occlusal views. Three times natural size.

PLATE 5

TRICENTES AND CHIRIACUS FROM THE BISON BASIN PALEOCENE

Figs. 1, 2. *Chriacus*, near *C. pelvidens* (Cope): 1, Right ramus of mandible (U.S.N.M. No. 20983), lateral and occlusal views; 2, left M²? (U.S.N.M. No. 21003), occlusal view. Two and one-half times natural size.
Fig. 3. *Chriacus*, sp: Left M²? (U.S.N.M. No. 21019), occlusal view. Two and one-half times natural size.
Fig. 4. *Tricentes fremontensis*, new species: Left ramus of mandible (U.S.N.M. No. 20582), type specimen, lateral and occlusal views. Two and one-half times natural size.

PLATE 6

THYRYPTACODON FROM THE BISON BASIN PALEOCENE

Fig. 1. *Thryptacodon belli*, new species: Right ramus of mandible (U. of Wyo. No. 1045), type specimen, lateral and occlusal views. Twice natural size.
Fig. 2. *Thryptacodon*, cf. *demari*, new species: Left maxilla (U.S.N.M. No. 20984), occlusal view. Twice natural size.
Fig. 3. *Thryptacodon demari*, new species: Right ramus of mandible (U.S.N.M. No. 20985), type specimen, lateral and occlusal views. Twice natural size.
Fig. 4. *Thryptacodon*, cf. *belli*, new species: Left maxilla (U.S.N.M. No. 20986), occlusal view. Twice natural size.
Fig. 5. *Thryptacodon*, cf. *australis* Simpson: Left ramus of mandible (U. of Wyo. No. 1076), occlusal and lateral views. Twice natural size.

PLATE 7

CLAENODON FROM THE BISON BASIN PALEOCENE

Figs. 1, 6. *Claenodon acrogenius*, new species: 1, Left ramus of mandible (U.S.N.M. No. 20575), occlusal view, natural size; 6, right ramus of mandible (U.S.N.M. No. 20634), type specimen, lateral view, one-half natural size.
Figs. 2, 3. *Claenodon*, cf. *ferox* (Cope): 2, Left ramus of mandible (U.S.N.M. No. 20633), occlusal view; 3, right maxilla (U.S.N.M. No. 20797), occlusal view. Natural size.
Fig. 4. *Claenodon*, cf. *montanensis* (Gidley): Left ramus of mandible (U.S.N.M. No. 20574), occlusal view. Natural size.
Fig. 5. *Claenodon*, cf. *procyonoides* (Matthew): Right ramus of mandible (U.S.N.M. No. 20630), lateral and occlusal views. Twice natural size.

PLATE 8

LITOMYLUS AND PROTOSELENE? FROM THE BISON BASIN PALEOCENE

- Figs. 1, 3. *Protosclene? novissimus*, new species: 1, Left ramus of mandible (U.S.N.M. No. 20572), type specimen, lateral and occlusal views; 3, right ramus of mandible (U.S.N.M. No. 21023), lateral and occlusal views. Four times natural size.
- Fig. 2. *Litomylus*, cf. *scaphicus*, new species: Right M¹ or M² (U.S.N.M. No. 21013), occlusal view. Four times natural size.
- Fig. 4. *Litomylus scaphicus*, new species: Right ramus of mandible (U.S.N.M. No. 21014), type specimen, lateral and occlusal views. Four times natural size.
- Fig. 5. *Litomylus scaphiscus*, new species: Right ramus of mandible (U.S.N.M. No. 21010), type specimen, lateral and occlusal views. Four times natural size.

PLATE 9

HAPLALETES AND GIDLEYINA FROM THE BISON BASIN PALEOCENE

- Fig. 1. *Haplaletes pelicatus*, new species: Left ramus of mandible (U.S.N.M. No. 21008), type specimen, lateral and occlusal views. Four times natural size.
- Fig. 2. *Haplaletes scrior*, new species: Left ramus of mandible (U. of Wyo. No. 1078), type specimen, lateral and occlusal views. Four times natural size.
- Figs. 3, 4. *Gidleyina wyomingensis*, new species: 3, Right ramus of mandible (U.S.N.M. No. 20790), type specimen, lateral and occlusal views; 4, right maxilla (U.S.N.M. No. 20795), occlusal view. Twice natural size.

PLATE 10

PHENACODUS? FROM THE BISON BASIN PALEOCENE

- Figs. 1-3. *Phenacodus? bisonensis*, new species: 1, Right ramus of mandible (U.S.N.M. No. 20567), lateral and occlusal views, 1½ times natural size; 2, right maxilla (U.S.N.M. No. 20564), type specimen, occlusal view, 1½ times natural size; 3, right maxilla (U.S.N.M. No. 20566), occlusal view, twice natural size.
- Figs. 4, 5. *Phenacodus? sp.* (large): 4, Right ramus of mandible (U.S.N.M. No. 21025), occlusal view, 1½ times natural size; 5, right P³ (U.S.N.M. No. 21038), occlusal view, twice natural size.

PLATE 11

CONDYLARTIIS AND TITANOIDES FROM THE BISON BASIN PALEOCENE

- Figs. 1, 2. *Promioclacnus pipiringosi*, new species: 1, Right ramus of mandible (U.S.N.M. No. 20571), type specimen, lateral and occlusal views; 2, right ramus of mandible (U.S.N.M. No. 21021), lateral and occlusal views. Four times natural size.
- Figs. 3, 4. *Litolestes lacunatus*, new species: 3, Left ramus of mandible (U.S.N.M. No. 21016), type specimen, lateral and occlusal views; 4, left ramus of mandible (U. of Wyo. No. 1079), lateral and occlusal views. Four times natural size.

Fig. 5. *Titanoides primaeus* Gidley: Right upper molars (U. of Wyo. No. 1093), occlusal view. Natural size.

PLATE 12

CAENOLAMBDA FROM THE BISON BASIN PALEOCENE

Caenolambda pattersoni, new genus and species: Skull (U.S.N.M. No. 21036), type specimen, dorsal view. One-half natural size.

PLATE 13

CAENOLAMBDA FROM THE BISON BASIN PALEOCENE

Caenolambda pattersoni, new genus and species: Skull (U.S.N.M. No. 21036), type specimen, lateral view. One-half natural size.

PLATE 14

CAENOLAMBDA FROM THE BISON BASIN PALEOCENE

Caenolambda pattersoni, new genus and species: Skull (U.S.N.M. No. 21036), type specimen, ventral view. One-half natural size.

PLATE 15

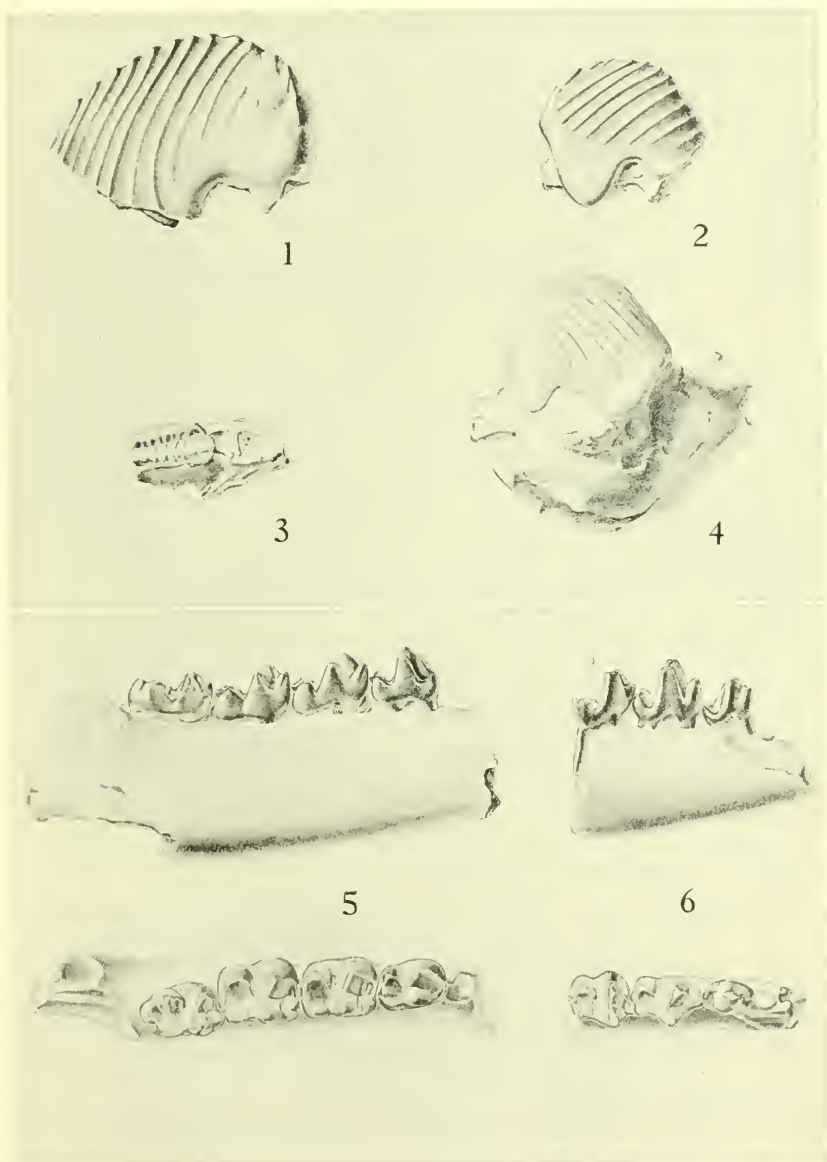
SOUTH RIM OF BISON BASIN SHOWING FOSSIL LOCALITIES

View westward along escarpment forming south rim of Bison basin. Fossil localities indicated are as follows: a, saddle locality; b, ledge locality; c, *Titanoides* locality; and d, west-end locality.

PLATE 16

TWO FOSSIL LOCALITIES IN THE BISON BASIN

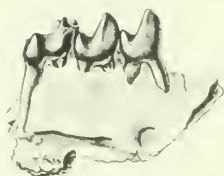
Above, view eastward of ledge locality (b). Below, view southwestward of west-end locality (d).



MULTITUBERCULATES AND INSECTIVORES FROM THE BISON BASIN PALEOCENE
(SEE EXPLANATION AT END OF TEXT.)



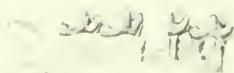
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PRIMATES AND MARSUPIALS FROM THE BISON BASIN PALEOCENE

(SEE EXPLANATION AT END OF TEXT.)



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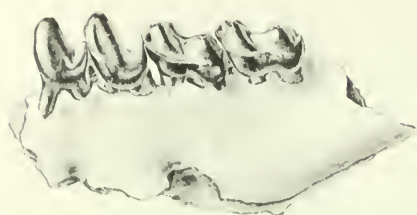
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PRONOTHODECTES FROM THE BISON BASIN PALEOCENE
(SEE EXPLANATION AT END OF TEXT.)



1



2



3



PLESIADAPIS FROM THE BISON BASIN PALEOCENE

(SEE EXPLANATION AT END OF TEXT.)



1



2



3



4



TRICENTES AND CHRIACUS FROM THE BISON BASIN PALEOCENE
(SEE EXPLANATION AT END OF TEXT.)



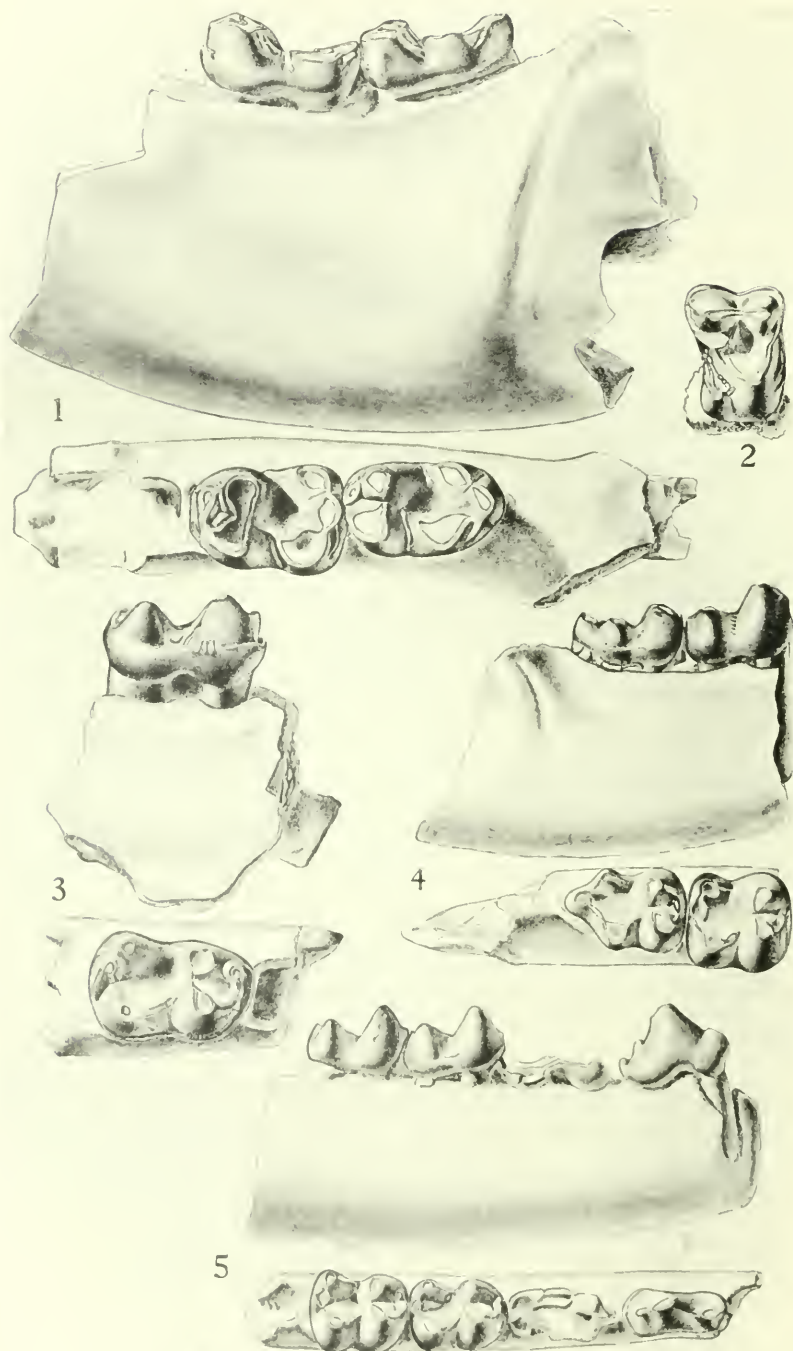
THRYPTACODON FROM THE BISON BASIN PALEOCENE

(SEE EXPLANATION AT END OF TEXT.)



CLAENODON FROM THE BISON BASIN PALEOCENE

(SEE EXPLANATION AT END OF TEXT.)



LITOMYLUS AND PROTOSELENE? FROM THE BISON BASIN PALEOCENE

(SEE EXPLANATION AT END OF TEXT.)



1



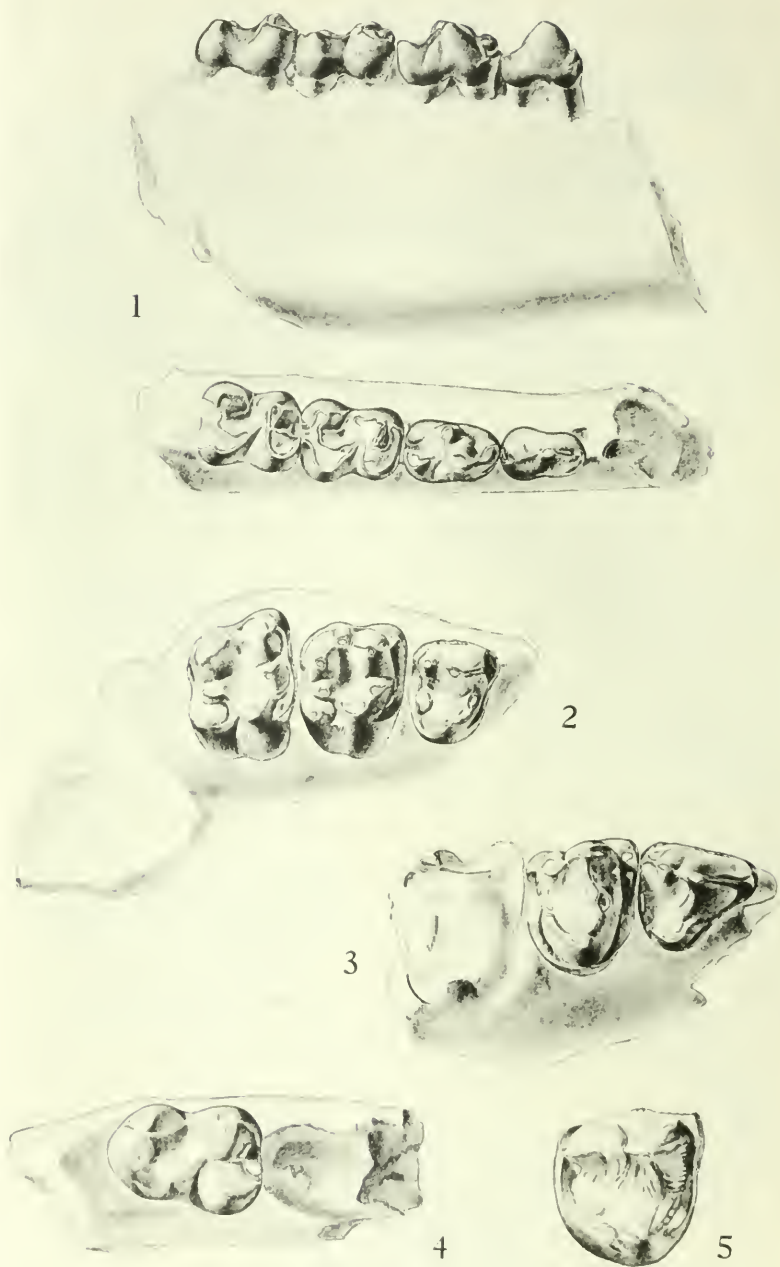
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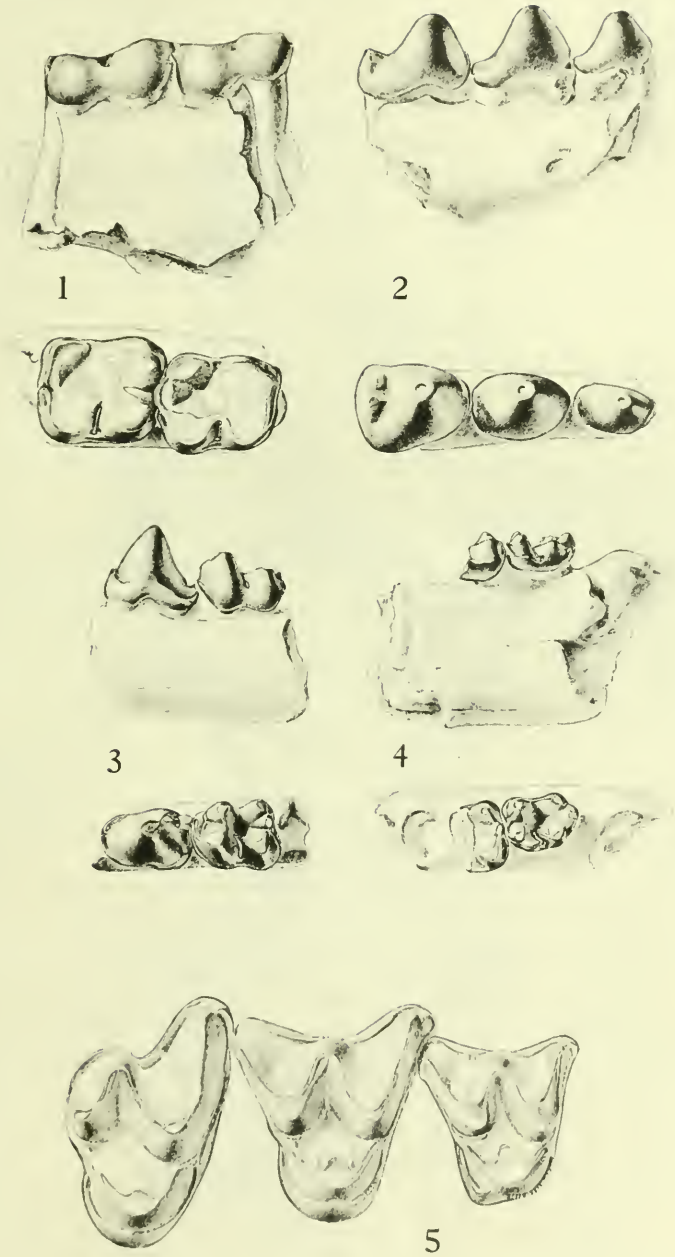


4



PHENACODUS? FROM THE BISON BASIN PALEOCENE

(SEE EXPLANATION AT END OF TEXT.)



CONDYLARTHS AND TITANOIDES FROM THE BISON BASIN PALEOCENE
(SEE EXPLANATION AT END OF TEXT.)



CAENOLAMBDA FROM THE BISON BASIN PALEOCENE

(SEE EXPLANATION AT END OF TEXT.)

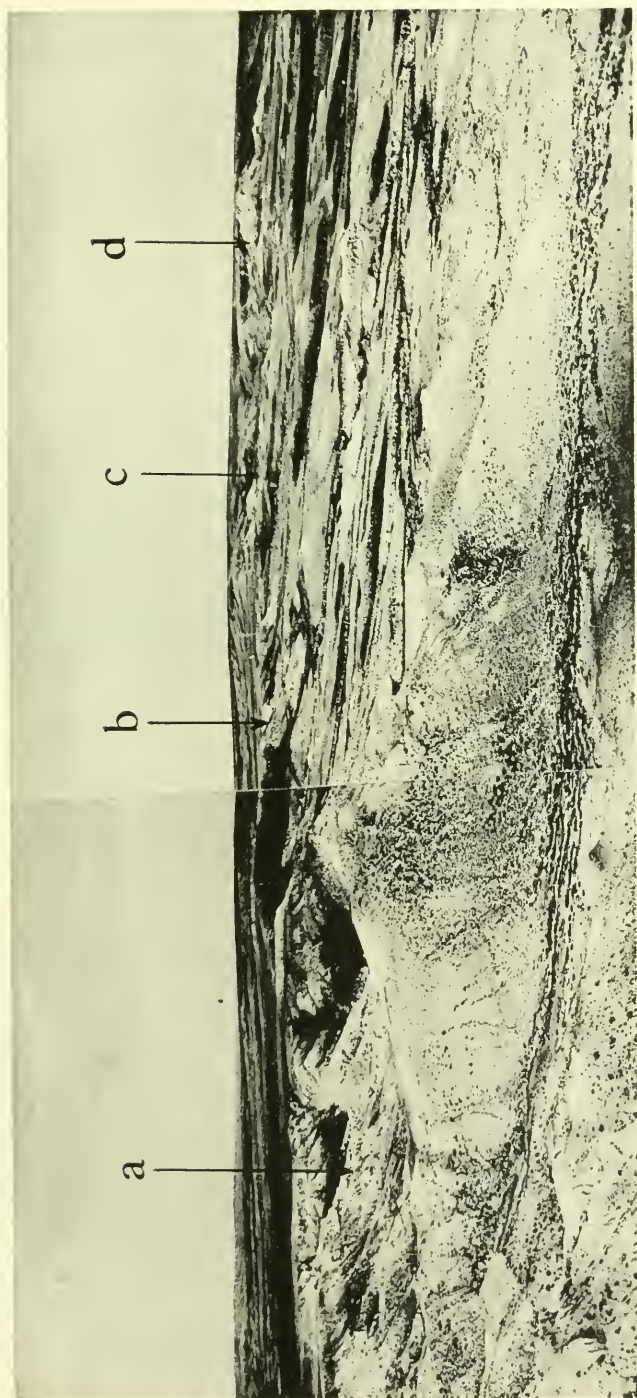


CAENOLAMBDA FROM THE BISON BASIN PALEOCENE
(SEE EXPLANATION AT END OF TEXT.)



CAENOLAMBDA FROM THE BISON BASIN PALEOCENE

(SEE EXPLANATION AT END OF TEXT.)



SOUTH RIM OF BISON BASIN SHOWING FOSSIL LOCALITIES

(SEE EXPLANATION AT END OF TEXT.)



TWO FOSSIL LOCALITIES IN THE BISON BASIN

(SEE EXPLANATION AT END OF TEXT.)

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 131, NUMBER 7

Charles D. and Mary Vaux Walcott
Research Fund

THE UPPER PALEOCENE MAMMALIA
FROM THE ALMY FORMATION IN
WESTERN WYOMING

(WITH 2 PLATES)

By

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ILLUSTRATIONS

PLATES

(Following p. 18)

1. Primates, *Anacodon?* and *Probathyopsis?* from the Almy Paleocene.
2. Condylarths from the Almy Paleocene.

Charles D. and Mary Vaux Walcott Research Fund

THE UPPER PALEOCENE MAMMALIA FROM
THE ALMY FORMATION IN
WESTERN WYOMING

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(WITH 2 PLATES)

INTRODUCTION AND HISTORY OF INVESTIGATION

Repeated, intensive search of a comparatively small exposure area of the Almy formation in western Wyoming has, over the past 15 years, resulted in a faunal representation of about a dozen mammalian species. This is, no doubt, a rather meager sample of the probable fauna although based on a little over 70 determinable specimens. It is, nevertheless, an interesting increase, from the original five forms recognized (Gazin, 1942) on but nine specimens. The Clarkforkian upper Paleocene age interpreted for the scant, earlier materials now seems clearly indicated by the collections as a whole.

The locality consists of a small cluster of closely adjacent exposures on the north side of La Barge Creek about 7 miles due west of the town of La Barge, formerly Tulsa P. O., in Lincoln County, Wyo. The most productive of these has been one in the vicinity of a topographic saddle, bare of vegetation, at the head of a ridge along the southeast side of Buckman Hollow (see advance sheet, U.S.G.S. La Barge quadrangle) in NW $\frac{1}{4}$ NE $\frac{1}{4}$ sec. 12, T.26 N., R.114 W. Other localities worthy of mention are on the southeast side of the above ridge, nearer the highway, and on the ridges to the northwest of Buckman Hollow in the vicinity of Spring Creek.

Discovery of these localities, as has been previously noted, was made by J. B. Reeside, Jr., B. N. Moore, and W. W. Rubey of the U. S. Geological Survey in 1936. Discovery by Rubey and John Rodgers in 1939 of *Plesiadapis* material at one of the sites provoked our interest, and in 1941 an additional small collection was made by

G. F. Sternberg, Franklin Pearce, and myself. The result of these early searches was the nine specimens described in the preliminary note of 1942. Smithsonian Institution parties revisited the localities in 1948, 1949, 1951, 1953, and 1954. On most of these expeditions I was assisted by the chief of our laboratory of vertebrate paleontology, Franklin L. Pearce. In 1948, I was aided by my wife, Elisabeth, and son, Chester. Chester Gazin also assisted Pearce and me in 1949.

The excellent pencil drawings of specimens shown in the two plates accompanying this report were made by Lawrence B. Isham, scientific illustrator for the Department of Geology in the National Museum.

GEOLOGIC RELATIONS AND OCCURRENCE OF REMAINS

Although the fossil-bearing beds on La Barge Creek have been mapped by A. R. Schultz (1914) as Almy, and are so regarded by Rubey¹ in his recent investigations of the region, it should be noted that the type section for the Almy formation, in the vicinity of Evans-ton, Wyo., is in a separate, although adjacent, basin of Tertiary deposition and there may have been no actual continuity between the two lithologically somewhat similar deposits.

The Almy formation is mapped in the Upper Green River Basin as a nearly continuous band along the east flank of the Wyoming Range from the vicinity of La Barge Creek to Fall River in the Hoback Basin. At La Barge Creek it appears and is shown by Schultz to be in depositional contact with lower Paleozoic rocks to the east and with upper Paleozoic and Triassic rocks forming the front of the range to the west. The Almy area immediately to the north of La Barge Creek is separated from the Eocene of the Green River Basin on the east by faulting, shown as a thrust by Schultz in which the lower Paleozoic beds underlying the Almy have ridden out over the younger rocks to the east. To the south of La Barge Creek the Paleozoic rocks which make up La Barge or Hogsback Ridge, together with the trace of the thrust fault, disappear beneath the Eocene of the Green River Basin, with the Knight formation extending westward to contact with the Almy, as it does again some distance to the north.

In the vicinity of the fossil occurrences the Almy beds are a reddish, pebbly clay, partly conglomeratic, dipping steeply to the southwest toward La Barge Creek. They appear to be nearly conformable

¹ Oral communication.

with the underlying Paleozoic limestones in Buckman Hollow, a relationship, of course, of a strictly local character. The various fossil sites are nearly all very low in the section and at the topographic saddle formed at the head of the ridge bounding Buckman Hollow on the southeast scattered remains were found to within only a few feet of the underlying limestone. A locality on the southeast side of this ridge and nearer the road, which produced the type of *Phenacodus almiensis*, would appear to be a little higher in the section. *P. almiensis*, however, is well represented by materials from the lowest levels so that the stratigraphic difference in this instance would not appear to have faunal significance.

THE ALMY FAUNA

There follows a listing of the forms encountered in the Almy collections and an indication of the number of specimens recognized as representing each:

PRIMATES:

Plesiadapidae:

<i>Plesiadapis rubeyi</i> Gazin.....	2
<i>Plesiadapis cookei</i> Jepsen.....	3
<i>Plesiadapis? pearcei</i> , new species.....	2

Carpolestidae:

<i>Carpolestes</i> , cf. <i>dubius</i> Jepsen.....	1
----------------------------------------------------	---

CARNIVORA:

Arctocyoniidae:

<i>Anacodon? nexus</i> , new species.....	1
-------------------------------------------	---

Mesonychidae:

<i>Dissacus</i> , sp.	2
----------------------------	---

Miacidae:

<i>Didymictis?</i> , sp.	1
-------------------------------	---

CONDYLARTHRA:

Phenacodontidae:

<i>Ectocion ralstonensis</i> Granger.....	13
<i>Ectocion</i> , cf. <i>osbornianum</i> (Cope).....	4
<i>Phenacodus almiensis</i> Gazin.....	32
<i>Phenacodus primaevus</i> Cope.....	10*

DINOCERATA:

Uintatheriidae:

<i>Probathyopsis?</i> , sp.	2
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* Eight of these are of a smaller form tentatively regarded as *P. p.*, cf. *intermedius*.

AGE AND CORRELATION OF THE FAUNA

The fauna above listed is beyond doubt a Clarkforkian assemblage. It is interesting to note, moreover, that all the genera, except *Car-*

polestes, and certain of the species are also lower Eocene. Nevertheless, this fact, together with the relative abundance of condylarths and *Plesiadapis*, and absence of the more common Eocene forms such as *Hyracotherium*, *Homogalax*, *Hyopsodus*, *Diacodexis*, *Pelycodus*, etc., is regarded as characterizing Clark Fork time.

It is of further interest that all the genera here recognized are also either Tiffanian or, as *Ectocion* and *Anacodon*, arbitrarily distinguished from Tiffanian ancestral forms. This is regarded as further characteristic of Clark Fork time, i.e., the bulk of the Clark Fork fauna is a survival of a certain selection of known Tiffanian lines with the appearance of very few new stems from elsewhere. It would appear then that recognition of Clarkforkian time as distinct from Tiffanian on a generic level is, as in comparison with the Eocene, somewhat negative in character, partly depending upon the absence of a number of forms comparatively common in the earlier beds but presumed to have become extinct. Nevertheless, the species for the most part are advanced over those of Tiffanian time and we have in the Almy, for example, such forms as *Plesiadapis cookei*, *Anacodon? nexus*, *Ectocion ralstonensis*, *E.*, cf. *osbornianum*, *Phenacodus almiensis* and *P. primaevus*. From the Clark Fork beds in the Big Horn Basin there may be added to this list of progressive species such forms as *Thryptacodon antiquus*, *Didymictis protenus*, *Haplomylus speirianus*, and a species of *Coryphodon*.

The further evidence given the distinctiveness of Clark Fork time by the first known appearance of tillodonts and palaeonodonts calls attention to the comparatively few new lines that appear, evidently introduced from some other area, in contrast with the strikingly large and important part of the Eocene fauna that appeared at the end of Clark Fork time. This emphasizes the appropriateness and, undoubtedly, formed part of the reasoning followed in regarding Clarkforkian as upper Paleocene rather than Eocene, thereby permitting factors of a regional or perhaps greater importance that must have affected the faunal distribution to be correlated with an important time boundary.

SYSTEMATIC DESCRIPTION OF THE MAMMALIAN REMAINS

PRIMATES

PLESIADAPIDAE

PLESIADAPIS RUBEYI Gazin, 1942

Plate 1, figure 10

No additional material of this species has been found since description of the original Geological Survey collection. Included is the type

(U.S.N.M. No. 16696), a right mandibular ramus with P_3 - M_2 , but lacking the trigonid of M_1 , and a left M^3 tentatively referred to *Plesiadapis rubeyi*.

P. rubeyi clearly belongs to the group of species that includes *P. gidleyi*, *P. fodinatus*, *P. dubius*, and probably *P. cookei*. It is remote from the distinctive *P. jepseni*-*P. anceps*-*P. rex* group or subgenus. It is, moreover, rather close to *P. fodinatus* which Jepsen (1930) described from the Silver Coulee horizon of the Polecat Bench sequence. There is a possibility that *P. rubeyi* is not specifically distinct from *P. fodinatus*; however, in view of the distinctly small size of M_1 , the anteroposteriorly shorter appearing summit of the trigonid of M_2 , and the comparatively slender premolars showing an incipient metaconid on P_4 (as in *P. dubius* rather than *P. fodinatus*), the species *P. rubeyi* would seem to be valid. Moreover, *P. fodinatus* is typically Tiffanian in age, regarded as represented in the Bison Basin deposits and Fossil Basin Evanston(?) as well as in the Polecat Bench, and survival of this species into Clarkforkian time, though likely, awaits demonstration.

The tentatively referred last upper molar (U.S.N.M. No. 16697) is distinctly large for the type lower jaw of *P. rubeyi* and is posterolingually expanded somewhat as in *P. fodinatus*. It is possible that this tooth represents *P. fodinatus*, but the evidence is rather meager and would not seem to justify separate listing. The tooth measures 4.3 mm. anteroposteriorly by 6.0 for the greatest transverse diameter.

MEASUREMENTS IN MILLIMETERS OF LOWER TEETH IN TYPE SPECIMEN OF
Plesiadapis rubeyi, U.S.N.M. NO. 16696

P_3 , anteroposterior diameter : transverse diameter.....	2.8 : 1.9
P_4 , anteroposterior diameter : transverse diameter.....	2.9 : 2.2
M_1 , transverse diameter of talonid.....	2.7
M_2 , anteroposterior diameter : transverse diameter of talonid.....	3.7 : 3.2

PLESIADAPIS COOKEI Jepsen, 1930

Plate 1, figures 5-8

In addition to the lower jaw of *Plesiadapis cookei* (U.S.N.M. No. 16698) found in 1941, a second lower jaw with all three molars and an isolated M^3 were found by Franklin Pearce while in the field with me in 1954. *Plesiadapis cookei* is truly gigantic in comparison with other Paleocene primates and is nearly as large as the upper Bridgerian *Notharctus robustior*. Direct comparison of these jaw materials with the type specimen in the collections of Princeton University shows near identity in size and character of the teeth for the

1941 specimen, verifying the tentative assignment of the Buckman Hollow Almy form made in 1942. U.S.N.M. No. 20785 has lower molars a little broader than in the type, perhaps more noticeable in M_3 , but no doubt this is within the range of individual variation.

The last upper molar (U.S.N.M. No. 21281) is considerably larger than that (No. 16697) tentatively assigned to *P. rubeyi* but relatively does not show so marked a posterior extension of the posterolingual portion. It is also less expanded in this respect than in the type material of *P. cookei*. Its measurements are 6.8 mm. anteroposteriorly by 9.8 for the greatest diameter.

MEASUREMENTS IN MILLIMETERS OF LOWER TEETH IN SPECIMENS OF
Plesiadapis cookei

	U.S.N.M. No. 16698	U.S.N.M. No. 20785
P_3 , anteroposterior diameter: transverse diameter...	5.2:3.7	
P_4 , anteroposterior diameter.....	5.3	
M_1 , anteroposterior diameter: transverse diameter of talonid	6.1:5.6
M_2 , anteroposterior diameter: transverse diameter of talonid	6.4:5.5	6.4:6.3
M_3 , anteroposterior diameter: transverse diameter of trigonid	10.5 ^a :...	10.0 ^a :6.2

^a Approximate.

PLESIADAPIS? PEARCEI,² new species

Plate I, figure 9

Type.—Right ramus of mandible (U.S.N.M. No. 20787), with M_1 and M_2 .

Horizon and locality.—Buckman Hollow Clarkforkian Paleocene on La Barge Creek, NW $\frac{1}{4}$ NE $\frac{1}{4}$ sec. 12, T.26 N., R.114 W., Lincoln County, Wyo.

Specific characters.—Size close to that of *Plesiadapis dubius*, but trigonids of lower molars narrower and talonids wider than in that species. Apices of cusps on trigonid more widely spaced transversely and entoconid of M_1 and M_2 distinctly more posterolingual in position.

Discussion.—The two lower jaw portions considered to represent this peculiarly distinctive form were at first allocated to *P. rubeyi* but their smaller size coupled with the lingually and backward-jutting entoconid position apparently precludes this possibility. The position of the entoconid gives the talonid of the first two lower molars a relatively marked width in contrast with the narrow trigonid, com-

² Named for Franklin L. Pearce who found the type specimen.

pared, for example, with *P. dubius*, which this form approaches in length of lower molars. Moreover, although the trigonid is narrower at its base than in *P. dubius*, the apices of the cusps are more widely spaced transversely, and in M_1 the paraconid is farther forward. In M_2 , however, the paraconid is not farther forward with respect to the metaconid than in *P. dubius*.

The peculiarities outlined above tempt speculation on the possibility that an undescribed genus is represented. I believe, however, that the differences here noted are probably of no greater significance than (and quite opposite in general tendency to) the markedly sloping outer walls of lower cheek teeth seen in the *P. jepseni*-*P. anceps*-*P. rex* group, presumably no more than subgeneric in importance.

MEASUREMENTS IN MILLIMETERS OF LOWER TEETH IN SPECIMENS OF
Plesiadapis? pearcei

	U.S.N.M. No. 20787 Type	U.S.N.M. No. 20786
M_1 , anteroposterior diameter	3.1	3.2
M_1 , transverse diameter of trigonid.....	2.1	2.0
M_1 , transverse diameter of talonid.....	2.5	2.5
M_2 , anteroposterior diameter.....	3.4	...
M_2 , transverse diameter of trigonid.....	2.4	...
M_2 , transverse diameter of talonid.....	2.8	...

CARPOLESTIDAE

CARPOLESTES, cf. DUBIUS Jepsen, 1930

Plate 1, figure 4

A carpolestid P_4 (U.S.N.M. No. 21280) in the collection can be closely matched in size by specimens of *Carpolestes dubius*. The tooth shows a high, uniformly convex crest in lateral view with scarcely discernible vertical ridges. There would appear to be about eight feeble serrations in advance of the position of the heel which is broken away. In lingual view the vertical ridges are a little more visible and the height of the crown is less, but with possibly less difference in height between the two sides than in the Polecat Bench material. The posterior portion of the lingual surface is gently concave, whereas the labial wall is slightly convex in vertical profile. In a dorsal view the crown appears slightly bilobed with the greatest width across the posterior portion. There is no distinct cingulum labially, and lingually a cingulum is perhaps feebly defined posteriorly.

The Almy tooth is distinctly larger and higher crowned than the corresponding tooth in *Carpodectes hazelae*. It also has a greater

number of serrations of smaller size and the associated ridges are less clearly defined. U.S.N.M. No. 21280 is certainly much closer to *Carpolestes dubius* than to any of the other known carpolestids, and it seems, moreover, that *C. dubius* is somewhat more removed from *Carpodaptus* in the form of P_4 than is the genotype *Carpolestes nigridentis*.

Carpolestes dubius is recorded by Jepsen (1930) from the Clark Fork beds as well as the Tiffanian portion of the Polecat Bench sequence.

The Almy P_4 measures 2.9 mm. from its anterior margin to the posterior root at the alveolus. The width is approximately 1.8 mm. across the posterior portion of the base of the tooth.

CARNIVORA

ARCTOCYONIDAE

ANACODON? NEXUS,³ new species

Plate 1, figure 1

Type.—Left ramus of mandible (U.S.N.M. No. 21282) with M_1 and M_2 .

Horizon and locality.—Buckman Hollow Clarkforkian Paleocene on La Barge Creek, NW $\frac{1}{4}$ NE $\frac{1}{4}$ sec. 12, T.26 N., R.114 W., Lincoln County, Wyo.

Specific characters.—Size considerably smaller than *Anacodon ursidens*, but teeth only slightly larger than in type of *Claenodon montanensis*. Primary cusp pattern of lower molars better defined than in *Anacodon ursidens* or *A. cultridentis*, but trigonid less elevated above talonid than in *Claenodon montanensis*. Also, anterior crest from hypoconid low but joins protoconid at a completely lingual position so that inner wall of first two lower molars shows little flexure mid-way of its length.

Discussion.—*Anacodon? nexus* is considered as possibly representing that genus rather than *Claenodon* as earlier (Gazin, 1956 and in press) supposed, because of the lowness of the trigonid on M_1 as well as M_2 . Also the crista obliqua has entirely lost its oblique character or has been overshadowed by the development of a distinctly lateral spur or crest extending forward from the hypoconid to the posterolateral surface of the protoconid, one of the several possibilities afforded by the crenulated character of the principal cusps in the

³ *nexus* (L.)=tie, bind, with reference to its intermediate position between *Claenodon* and *Anacodon*.

Claenodon line. The result of this is a broadening of the basin of the talonid giving it a rather different appearance than, for example, in *Claenodon montanensis*. Nevertheless, the lower molars have retained clear definition of the principal cusps, showing the *Claenodon* pattern, which is nearly lost in the crenulate character of the more flattened tooth crowns of Eocene *Anacodon*.

The character of the anterior portion of the jaw in *Anacodon?* *nexus* cannot be determined, nevertheless the reduction of the anterior premolars, the development of a diastema behind the canine, and a flange on the lower jaw below the symphysis characteristic of *Anacodon* has already been anticipated in *Claenodon acrogenius* of the lower Tiffanian in the Bison Basin. However, in *C. acrogenius* the flange is comparatively incipient and the lower canine is enlarged rather than reduced. Moreover, the lower molars of *C. acrogenius*, except for size, would appear to be indistinguishable from those in other species of *Claenodon*. I suspect that the anterior portion of the lower jaw of *Anacodon?* *nexus* was deepened and exhibited a diastema behind the canine, although this is not certain, and there remains the possibility that *A.?* *nexus* is a survival of more typical *Claenodon* with shallow symphysis and unreduced premolars, but with the tooth pattern advancing parallel to that leading to *Anacodon*.

M₁ in No. 21282 of *Anacodon?* *nexus* measures approximately 9.5 mm. in length by 7.8 mm. across the talonid. M₂ is about 10.7 mm. long and 8.5 mm. across the trigonid.

MESONYCHIDAE

DISSACUS, sp.

The upper tooth portion (U.S.N.M. No. 16699) including the protocone and metacone, previously (Gazin, 1942) listed as a "creodont, gen. and sp. undet.," may well be an anterior molar of *Dissacus*. A second tooth fragment, the posterior portion of a lower premolar, possibly P₂ or P₃, also suggests *Dissacus*. These are evidently of a form not greatly different in size from the Torrejonian *Dissacus navajovius*, clearly smaller than *Dissacus praenuntius* Matthew of the Clark Fork beds.

MIACIDAE

DIDYMICTIS?, sp.

A left M₁ may well belong to a species of *Didymictis*, but is very much smaller than contemporary *Didymictis protenus proteus* from

the Clarkforkian of the Big Horn Basin. It is only a little smaller than Torrejonian *Didymictis haydenianus*, but not to be compared with *D. microlestes* or *D. tenuis*. Possibly the Almy form is a forerunner of one of the other miacid genera of the Eocene, but the tooth in question is not too well preserved so that detailed comparison is unwarranted.

CONDYLARTHRA

PHENACODONTIDAE

ECTOCION RALSTONENSIS Granger, 1915

Plate 2, figures 1 and 2

Ectocion, though by no means as abundantly represented in number of specimens as *Phenacodus*, has in the material comprising it certainly the best specimen in the Almy collection. The skull and jaws (U.S.N.M. No. 20736) referred to *Ectocion ralstonensis* in general lack only the right and posterior elements of the cranium and the posterior portion of the right ramus of the mandible. The rostrum and left side of the cranium and mandible are comparatively well preserved, though fractured and slightly distorted. The teeth are for the most part in excellent condition and only the upper incisors and P¹ and P² of the right side are missing from the skull. The lower jaws have P₃-M₃ preserved in both rami. An incomplete humerus and ulna were found associated with the skull. There are, in addition to this specimen, about 12 others consisting of jaw and maxillary portions and isolated teeth referred to or tentatively identified as *E. ralstonensis* in the Almy collection.

In a lateral aspect the *Ectocion ralstonensis* skull reveals certain details of interest regarding the foramina, so often not ascertainable in Paleocene materials. The anterior opening of the infraorbital foramen is directly above the anterior root of P³ and well forward of the anterior margin of the orbit. Posteriorly this foramen opens in the orbital cavity at the anterior apex of the large triangular-shaped orbital plate of the maxilla. Superior and somewhat medial to the posterior opening of the infraorbital foramen and separated from it by a backward and medially extending ridge, which may coincide with the sutural ridge of the maxilla, is an aperture believed to be a sphenopalatine foramen. Above this and somewhat lateral to it is the lachrymal foramen, concealed in lateral view by the margin of the orbit.

In the posterior portion of the orbital cavity, the optic foramen is well forward—a little less than a centimeter—of the sphenoidal fis-

sure. About a half centimeter posterolateral and somewhat ventral to the sphenoidal fissure is an aperture which is surely the anterior opening of an alisphenoid canal. The posterior opening is clearly defined well forward and ventromedial to the foramen ovale. I am unable to determine the presence or absence of a foramen rotundum, possibly opening into the alisphenoid canal. According to W. K. Gregory (Orders of Mammals, p. 354), a foramen rotundum opened into the alisphenoid canal in *Phenacodus*; however, Simpson (1933), in describing an endocranial cast of *Phenacodus*, shows both first and second branches of the trigeminal nerve as having passed through the sphenoidal fissure. This would seem to preclude the possibility of a distinctly separate foramen rotundum in *Phenacodus*, which is regarded as closely related to *Ectocion*.

Ventrally, the posterior palatine foramen is about opposite the posterolingual portion of M_1 . There is a small, blunt pterygoid process of the maxilla, and opposing it medially is a somewhat everted lateral portion of the anterior margin of the posterior narial aperture. The nasal cavity is closed below posteriorly to a position about even with the posterior margin of the last molar. The previously mentioned posterior opening of the alisphenoid canal faces more ventrally and well ahead of the foramen ovale, a relative distance nearly as great as in *Meniscotherium*. The postglenoid foramen is large and placed posteromedial to the postglenoid process, and the space for the audital tube behind the postglenoid process is shallow and broadly open.

The teeth in U.S.N.M. No. 20736 show the anterior premolars, above and below, to be separated from each other and from the canine by diastemata, the greatest separation being between the first and second premolars, about 4 mm. above and 3 mm. below. The anterior premolars above are simple and 2-rooted, whereas P_1 has but one root.

The essential difference between *Ectocion ralstonensis*, as exemplified by No. 20736, and the *Ectocion osbornianum* material in the U. S. National Museum from the Gray Bull is to be found, in addition to a slightly smaller size of the teeth, in the less progressive character of the posterior premolars of *E. ralstonensis*. The tritocone in both P^3 and P^4 is distinctly less developed and less well separated from the primary cusp. This is particularly noticeable in P^3 . Moreover, the anterointernal cusp or protoconule is less developed. It is not present on P^3 and comparatively weak on P^4 of *E. ralstonensis*. In *E. osbornianum* material at hand, the protoconule is generally prominent and may be thrust to a decidedly anterolingual position in both P^3 and P^4 . There is no tetartocone on the posterior upper premolars of

No. 20736, but it may be moderately developed on the cingulum of P^4 and sometimes P^3 in *E. osbornianum*.

The lower premolars appear relatively more slender in *Ectocion ralstonensis* than in *E. osbornianum*, and P^4 has a less molariform appearing talonid with, as noted by Granger (1915, p. 353), a much weaker entoconid than usually seen in *E. osbornianum*; also *E. ralstonensis* exhibits a shallower mandible.

Upper and lower molars of *Ectocion ralstonensis* are apparently not distinctive in comparison with *E. osbornianum*, except for the greater average size in the latter. However, comparison with *Gidleyina wyomingensis* (Gazin, 1956) shows that, as earlier stated, the crests from the protocone to the protoconule and metaconule of the upper molars are better defined in the latter. Moreover, in some specimens of *Gidleyina wyomingensis* and in the types of *G. silberlingi* and *G. superior* the parastylid crest of the lower molars tends to join the metaconid, suggestive of *Phenacodus*. As noted by Granger, the parastylid crest of *Ectocion*, as far as observed, is separate from the metaconid in the lower molars.

MEASUREMENTS IN MILLIMETERS OF DENTITION IN SPECIMEN OF
Ectocion ralstonensis, U.S.N.M. NO. 20736

Length of upper dentition from anterior margin of canine (at alveolus) to posterior margin of M^3	49.7
Length of upper cheek tooth series, P^1 - M^3 , inclusive.....	41.8
Length of upper premolar series, P^1 - P^4 , inclusive.....	24.0
Length of upper molar series, M^1 - M^3 , inclusive.....	18.0
C, anteroposterior diameter at alveolus: transverse diameter at alveolus.	4.1: 2.8
P^1 , anteroposterior diameter: transverse diameter.....	3.0: 1.5
P^2 , anteroposterior diameter: transverse diameter.....	4.0: 2.2
P^3 , anteroposterior diameter: transverse diameter.....	5.7: 5.5
P^4 , anteroposterior diameter: transverse diameter.....	6.0: 7.3
M^1 , anteroposterior diameter: transverse diameter across anterior portion	6.2: 8.5
M^2 , anteroposterior diameter: transverse diameter across anterior portion	6.2: 9.1
M^3 , anteroposterior diameter: greatest transverse diameter.....	4.9: 7.5
Length of lower cheek tooth series P_1 (at alveolus)- M_3 , inclusive.....	42.8
Length of lower premolar series, P_1 (at alveolus)- P_4 , inclusive.....	23.3
Length of lower molar series, M_1 - M_3 , inclusive.....	20.0
P_3 , anteroposterior diameter: transverse diameter.....	5.5: 3.2
P_4 , anteroposterior diameter: transverse diameter.....	6.7: 4.1
M_1 , anteroposterior diameter: transverse diameter of talonid.....	6.5: 5.1
M_2 , anteroposterior diameter: transverse diameter of trigonid.....	6.5: 5.4
M_3 , anteroposterior diameter: transverse diameter of trigonid.....	6.7: 4.5

ECTOCION, cf. OSBORNIANUM (Cope), 1882

A right lower jaw fragment with P_4 - M_2 (U.S.N.M. No. 20645) has teeth more robust than in the jaw belonging to the *E. ralstonensis* skull, and in addition P_4 is more progressive with a better developed talonid basin and a large entoconid. P_4 , moreover, has a rather distinctly developed paraconid or parastylid. This specimen is tentatively regarded as representing the Gray Bull species *E. osbornianum*. There are in addition three other jaw fragments, each with a comparatively large molar which may likewise be referred.

Although Granger (1915) recognized three species of *Ectocion* in the Clark Fork beds, including both *E. ralstonensis* and *E. osbornianum*, Simpson (1937b), in his treatment of the material, believed (except for rare *E. parvus*) that a single species was represented in which there was a shift in the mean size, the length of M_1 for example, between successive horizons from Clark Fork to Lost Cabin time. While this seems evident in the demonstration given, I am, nevertheless, concerned about the more progressive P_4 in the larger Almy specimen. The character of P_4 might likewise show marked variation within a species, but there are three small-toothed or *E. ralstonensis* specimens which have P_4 preserved, and in each of these this tooth is distinctly less progressive. The correlation may be a coincidence, but if not, I am inclined to believe that in this instance a distinct species is actually represented.

MEASUREMENTS IN MILLIMETERS OF TEETH IN THE SPECIMEN OF
Ectocion, cf. *osbornianum*, U.S.N.M. NO. 20645

P_4 , anteroposterior diameter:transverse diameter of talonid.....	7.5:5.1
M_1 , anteroposterior diameter:transverse diameter of trigonid.....	6.8:5.9
M_2 , anteroposterior diameter:transverse diameter of trigonid.....	7.1:6.5

PHENACODUS ALMIENSIS Gazin, 1942

Plate 2, figures 3 and 4

A relatively small species of *Phenacodus*, *P. almiensis*, is clearly the most abundantly represented form in the fauna. The 32 specimens in the collection referred to it comprise about 44 percent of the total. The type specimen, U.S.N.M. No. 16691, consists of maxillae with the canines and P^3 to M^3 in a scarcely worn state, together with certain limb and vertebral portions. Although collected in 1941, it remains after six subsequent collecting trips the best specimen of this species extant.

P. almiensis is much smaller than *Phenacodus p. intermedius* but appreciably larger than *P. copei*. It differs essentially from the *Phenacodus primaevus* group, other than in size, in better developed external styles, particularly the parastyle, and in exhibiting slightly more crescentic cusps. The protocone in the upper molars, for example, is united by better defined crests to the protoconule and metaconule and generally with the hypocone as well. The metaconule is about on a line between the metacone and hypocone, not posterior to this, as frequently observed in *P. primaevus*, nor so forward as in *Ectocion*.

P. almiensis is significantly larger than any of the *P. copei* material observed, and although the latter exhibits fairly prominent external styles on the upper molars, the cusps, particularly the protocone, have less developed crests than in *P. almiensis*. Granger (1915) noted that the metaconules were weak or absent in *P. copei*. These are apparently not reduced in *P. almiensis*. Moreover, the upper premolars, strangely enough, appear more advanced than in *P. copei*. P³ has a well-defined and separate tritocone, described as weak in *P. copei*, and this tooth in *P. almiensis* also has incipient to clearly defined conules and tetartocone. P⁴ is distinctly molariform in appearance, and is recognized among isolated teeth by the absence of a mesostyle and by the somewhat less developed, though by no means weak, hypocone (or tetartocone, in upper premolar nomenclature). Both conules are present and well defined.

Compared to earlier species, *P. almiensis* is distinctly larger than *P. matthewi*, as well as *P. gidleyi*, and not nearly so robust as *P. grangeri* among the species known from the Colorado Tiffany. Moreover, the teeth are relatively not so broad transversely as in *P. grangeri*. The premolars are decidedly more advanced than in *Phenacodus bisonensis*.

As noted earlier (Gazin, 1942), the teeth of *P. almiensis* show some resemblance to *Ectocion* in the development of the external styles and somewhat crescentic appearance of the cusps; however, I do not believe that *Ectocion* is represented because of the markedly elongate (anteroposteriorly) and relatively narrow upper molars, the position of the metaconule, and the comparatively unreduced condition of the hypocone of M³. Also, in the lower molars the anterior crest joins both the protoconid and metaconid, and the hypoconulid is not so close to the entoconid as it usually is in *Ectocion*.

MEASUREMENTS OF UPPER TEETH IN SPECIMENS OF
Phenacodus almiensis

	U.S.N.M. No. 16691 Type	U.S.N.M. No. 21286
Length of cheek tooth series, P ³ -M ³ , inclusive.....	42.7 ^a	41.0 ^a
Length of molar series, M ¹ -M ³ , inclusive.....	26.1 ^a	26.7
P ³ , anteroposterior diameter: transverse diameter.....	8.2:7.4	7.7 ^a :8.6
P ⁴ , anteroposterior diameter: transverse diameter.....	8.5:8.5	7.9:9.2
M ¹ , anteroposterior diameter: transverse diameter *.....	9.0:10.0	9.0:11.0 ^a
M ² , anteroposterior diameter: transverse diameter *.....	9.2:11.3	8.8:12.5 ^a
M ³ , anteroposterior diameter: transverse diameter *.....	7.7:10.8	8.7 ^a :10.5 ^a

^a Approximate.

* Anteroposterior diameter of upper molars taken perpendicular to anterior margin and transverse diameter across anterior portion.

PHENACODUS PRIMAEVUS Cope, 1873

Plate 2, figure 5

Two specimens in the collection may well represent typical *Phenacodus primaevus*. One of these, U.S.N.M. No. 21287, is a lower jaw with P₃ to M₂, inclusive, and the other an incomplete lower molar. The teeth in No. 21287 are comparable in size to those in the Clark Fork material referred to *P. primaevus*. The length of the lower molars is near the lower limit of the range given for each (Simpson, 1937b, p. 18) and the widths are nearer the upper limit, suggesting relatively broad teeth, not otherwise distinguished from *P. primaevus*.

About eight specimens of smaller size, though not comparable to *P. almiensis*, correspond in general proportions to Gray Bull materials earlier regarded as *Phenacodus intermedius*. The dimensions of teeth in one of these (U.S.N.M. No. 20644), evidently the largest of the group, are given in the accompanying table. In this and others having comparable lower molars the teeth are observed to be relatively slender, particularly in comparison with the larger, broad-toothed form discussed above. A single specimen encountered by Simpson (1937b, p. 19) in the Clark Fork collections, representing a smaller group which approximates the intermediate-sized form in the Almy fauna, was regarded by him as *Phenacodus primaevus*, small var., cf. *intermedius*. The Almy materials may be treated in a similar manner, for taxonomic convenience, because, although the limited Almy materials might appear to be clearly defined, I find it difficult to distinguish *P. intermedius* from *P. primaevus* in the Gray Bull collections. Nevertheless, I feel rather strongly opposed to a concept which recognizes more than one subspecies of the same form coexisting in time and at the same geographic locality.

MEASUREMENTS IN MILLIMETERS OF CERTAIN LOWER TEETH IN JAWS OF

Phenacodus

	<i>P. almiensis</i> U.S.N.M. No. 20643	<i>P. p., cf. intermedius</i> U.S.N.M. No. 20644	<i>P. p. primacvus</i> U.S.N.M. No. 21287
P ₄ , anteroposterior diameter	9.6	11.5	12.7
P ₄ , transverse diameter of talonid	6.2	7.8	10.2
M ₁ , anteroposterior diameter	9.1	11.8	12.1
M ₁ , transverse diameter of talonid . . .	7.4	9.8	11.2
M ₂ , anteroposterior diameter	12.5 ^a
M ₂ , transverse diameter of trigonid	12.5

^a Approximate.

DINOCERATA

UINTATHERIIDAE

PROBATHYOPSIS?, sp.

Plate 1, figures 2 and 3

Two upper premolars, possibly both P³, or P³ and P⁴, but of different individuals as indicated by wear, are evidently of *Probathyopsis*. They are, however, significantly larger than *Probathyopsis praecursor* Simpson (1929) of the Clark Fork beds. They correspond closely in size to a P³ belonging with a partial skeleton of cf. *Bathyopsis fissidens* Cope from the New Fork upper Wasatchian (Gazin, 1952, p. 64), but are slightly more brachydont. The unworn Almy premolar (U.S.N.M. No. 21283) measures 14.6 mm. long perpendicular to anterior margin by 16.5 mm. wide perpendicular to outer wall. P³ in the type of *P. praecursor* measures 11.5 by 13.3 mm. in the same directions.

The proportions of the upper premolars are comparable to those of the earlier *Bathyopsoides harrisorum* Patterson (1939) from the Plateau Valley beds, although the unworn Almy premolar is a little shorter anteroposteriorly and broader transversely than the *B. harrisorum* P³. Nevertheless, the transverse lophs have about the same proportions. Although Patterson has indicated certain differences in cusp pattern of M₂, it would seem from the evidence presented by Dorr (1952, p. 89) that *Bathyopsoides* is possibly a male *Probathyopsis*. Better evidence with regard to this situation should be forthcoming in the more detailed study of the Hoback Basin material contemplated by Dorr.

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EXPLANATION OF PLATES

PLATE I

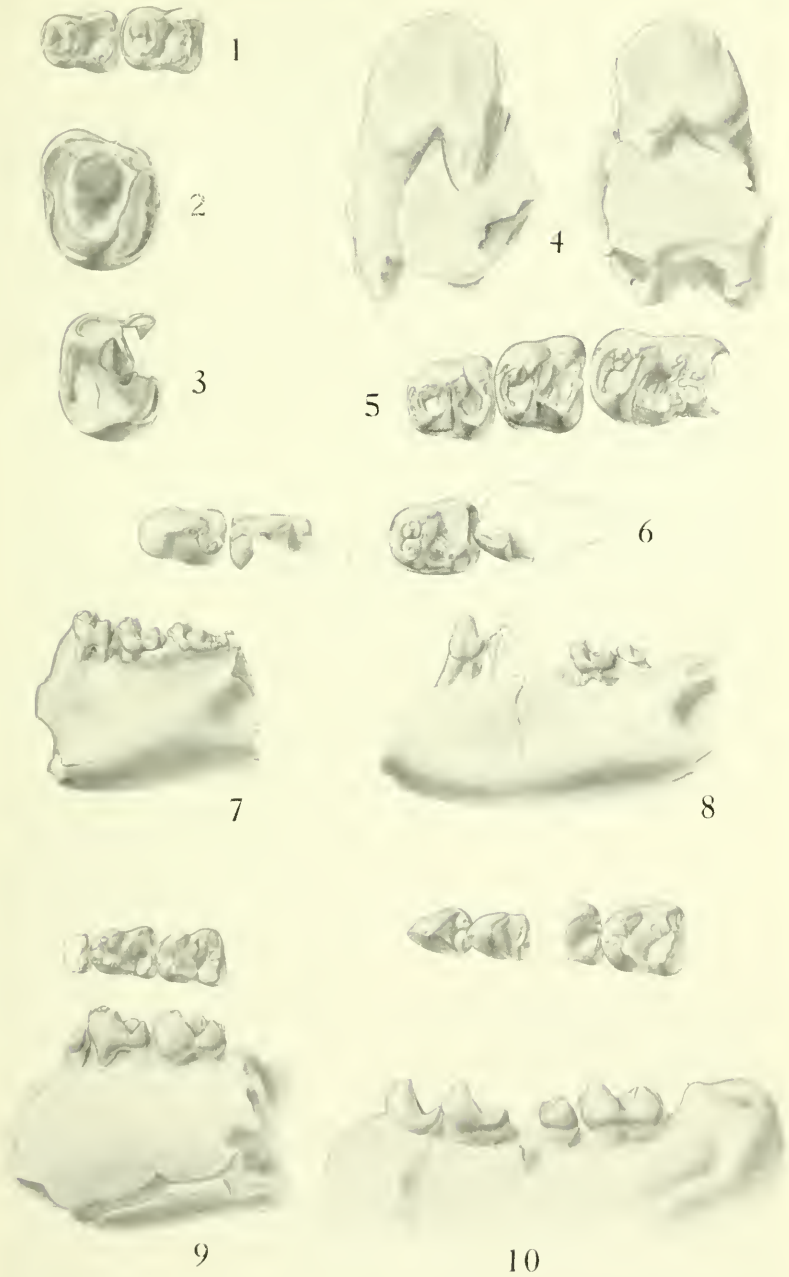
PRIMATES, ANACODON?, AND PROBATHYOPSIS? FROM THE ALMY PALEOCENE

- Fig. 1. *Anacodon? nexus*, new species: M₁ and M₂ (U.S.N.M. No. 21282), type specimen, occlusal view. Natural size.
- Figs. 2 and 3. *Proathyopsis?*, sp.: 2, Upper premolar (U.S.N.M. No. 21283), occlusal view; 3, upper premolar (U.S.N.M. No. 21284), occlusal view. Natural size.
- Fig. 4. *Carpolestes*, cf. *dubius* Jepsen: P₄ (U.S.N.M. No. 21280), labial (left) and lingual views. Six times natural size.
- Figs. 5-8. *Plesiadapis cooki* Jepsen: 5 and 7, Left ramus of mandible (U.S.N.M. No. 20785), (5) occlusal view, twice natural size, and (7) lateral view, natural size; 6 and 8, left ramus of mandible (U.S.N.M. No. 16698), (6) occlusal view, twice natural size, and (8) lateral view, natural size.
- Fig. 9. *Plesiadapis? pearcei*, new species: Right ramus of mandible (U.S.N.M. No. 20787), type specimen, occlusal and lingual views. Three times natural size.
- Fig. 10. *Plesiadapis rubeyi* Gazin: Right ramus of mandible (U.S.N.M. No. 16696), type specimen, occlusal and lingual views. Three times natural size.

PLATE 2

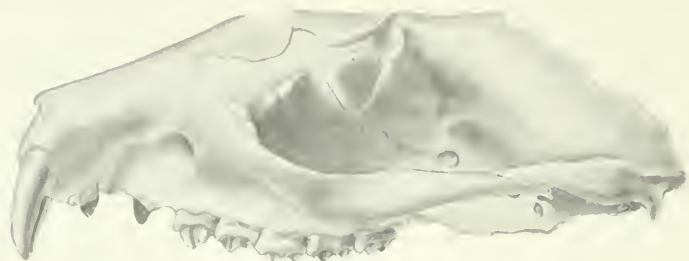
CONDYLARTHS FROM THE ALMY PALEOCENE

- Figs. 1 and 2. *Ectocion ralstonensis* Granger: 1, Skull (U.S.N.M., No. 20736), lateral and ventral views. Natural size; 2, left ramus of mandible (U.S.N.M. No. 20736), lateral and occlusal views (M₁ restored from right side). Natural size.
- Figs. 3 and 4. *Phenacodus almiensis* Gazin: 3, Right upper cheek tooth series (U.S.N.M. No. 16691), type specimens, occlusal view (M² restored from left side); 4, left ramus of mandible (U.S.N.M. No. 20643), occlusal view. Natural size.
- Fig. 5. *Phenacodus primaevus* Cope: Left ramus of mandible (U.S.N.M. No. 21287), occlusal view. Natural size.



PRIMATES, ANACODON?, AND PROBATHYOPSIS? FROM THE
ALMY PALEOCENE

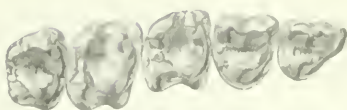
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2



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5

CONDYLARTHS FROM THE ALMY PALEOCENE

(SEE EXPLANATION AT END OF TEXT.)

SMITHSONIAN MISCELLANEOUS COLLECTIONS
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Charles D. and Mary Vaux Walcott
Research Fund

THE GEOLOGY AND VERTEBRATE
PALEONTOLOGY OF UPPER EOCENE
STRATA IN THE NORTHEASTERN
PART OF THE WIND RIVER
BASIN, WYOMING

PART 2. THE MAMMALIAN FAUNA OF THE
BADWATER AREA

(WITH 3 PLATES)

By

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Charles D. and Mary Vaux Walcott Research Fund
THE GEOLOGY AND VERTEBRATE PA-
LEONTOLOGY OF UPPER EOCENE
STRATA IN THE NORTHEASTERN
PART OF THE WIND RIVER
BASIN, WYOMING

PART 2.¹ THE MAMMALIAN FAUNA OF
THE BADWATER AREA

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(WITH 3 PLATES)

INTRODUCTION

The significance of the Wind River Basin in contributing information on mammalian faunas of upper Eocene time has been appreciated only during comparatively recent years. Although a rather meager fauna had been known from beds of Uintan equivalence below the Beaver Divide along the south side of the basin for many years, it is rather surprising that the occurrences on the north side were not earlier discovered, particularly in view of the long history of collecting associated with the adjacent lower Eocene Wind River formation. Discovery of the occurrence of upper Eocene mammalian remains along Badwater Creek near the site of the old Badwater Post Office by Wood, Seton, and Hares in 1936 was followed by investigations of others, notably those of Harry A. Tourtelot for the U. S. Geological Survey and parties for the Smithsonian Institution.

The present study stems largely from an interest in Eocene tapirids, the upper Eocene representatives of which are so well represented here, and is in part a sequel to an earlier review of artiodactyls

¹ Part 1 of this paper is a study of the geologic relations, in preparation by Harry A. Tourtelot.

of this age. Misunderstandings in the past as to the characteristics and, in some instances, the age of related types, largely from inadequate original descriptions of forms in these two ungulate groups, early confused the picture and resulted in incorrect identifications and evidently misleading conclusions as to the horizon represented by the Badwater assemblage. It is hoped that the present review and revision will clarify the record and render more useful the information to be derived from this occurrence.

ACKNOWLEDGMENTS

I am particularly indebted to Dr. G. Edward Lewis of the U. S. Geological Survey for relinquishing to me for restudy this very interesting assemblage, and assuring me that no embarrassment would ensue. I wish also to acknowledge the helpful information furnished me by Harry A. Tourtelot both in the office and in the field. Tourtelot, obligingly and with contagious enthusiasm, showed me the more significant and likely collecting sites during our 1946 field exploration.

Investigation was immeasurably aided by my being permitted to examine and study related materials in universities and other museums, and by the loan of pertinent specimens in these collections for direct comparison. Acknowledgment is particularly due Dr. J. LeRoy Kay at the Carnegie Museum, Dr. Glenn L. Jepsen at Princeton University, Dr. George G. Simpson at the American Museum, and Dr. Joseph T. Gregory at Yale Peabody Museum. Dr. H. E. Wood, II, aided in furnishing information on materials in the original Badwater collection.

The exquisite pencil drawings depicting selected materials shown in plates 1-3 were prepared by Lawrence B. Isham, staff artist for the Department of Geology in the U. S. National Museum. Mr. Isham also prepared the chart showing the tapiroid sequence.

HISTORY OF INVESTIGATION

Discovery of upper Eocene vertebrate materials in the Badwater area was made by Wood, Seton, and Hares, as reported by them in 1936. Moreover, this would appear to be the first record for the occurrence of upper Eocene on the north side of the Wind River Basin. Recognized by Wood, Seton, and Hares were *Amynodon advenus*, *Telmatherium*, cf. *cultridens*, and a crocodile. Collections later (1942) secured by J. D. Love and G. E. Lewis from Lysite Mountain to the north of Badwater Creek, for Yale University, include remains identified by Lewis as *Telmatherium*, cf. *cultridens*, and an indeterminate

helaetid (this is *Dilophodon*). Nevertheless, significant collections, more representative of the fauna, were not obtained from these beds until Harry A. Tourtelot and his assistants secured for the U. S. Geological Survey in 1944 and 1945 the materials discussed in his maps and reports of 1946, 1948, and 1953. Identification of the Geological Survey material was made by G. E. Lewis and reported by him in 1947. Collections for the Smithsonian Institution were made by F. L. Pearce, Chester Gazin, and myself in 1946, and Pearce and I revisited the localities with good results in 1953. Other known collections include that made by A. E. Wood in 1948 for Amherst College, the small mammals represented having been described by him in 1949. Further collecting was done by Tourtelot and the unusual *Malaquiferus tourteloti* skull was found by him near Dry Creek in 1948. Materials secured by the U. S. Geological Survey also included a collection made by J. R. Hough in 1950, and in her 1955 report on the Sage Creek occurrence comparisons are made with portions of the Badwater fauna.

OCCURRENCE AND PRESERVATION OF MATERIAL

The principal occurrences for materials of the Badwater fauna are the low gray-green exposures along the south side of Badwater Creek between $2\frac{1}{2}$ and $3\frac{1}{2}$ miles almost due northwest of the site of the now abandoned Badwater Post Office. These are immediately to the south and to the southeast of the mouth of Clear Creek in the southeast part of section 14, the southwest part of section 13, and the northwest part of section 24, T. 39 N., R. 89 W. The above, together with other scattered localities, are shown on both the 1946 and 1953 maps of Tourtelot, as well as his map accompanying part 1 of this study.

The discovery of Badwater vertebrate remains by Wood, Seton, and Hares was made at a locality south of Badwater P.O. about 3 miles to the southeast of the above exposures and in section 32, T. 39 N., R. 88 W. Determinable remains have likewise been encountered on Lysite Mountain to the north of the Badwater area by Lewis and Love, probably in section 25, T. 42 N., R. 90 W. The Dry Creek exposures, almost certainly the same age as those on Badwater Creek, are about 20 miles due west and include the sites for the *Malaquiferus* and *Eomoropus* skulls, in the NW $\frac{1}{4}$ sec. 14 and the SE $\frac{1}{4}$ sec. 9, respectively, T. 39 N., R. 92 W.

Much of the fossil material encountered has been rather fragmentary although there are five comparatively good skulls in the National Museum-Geological Survey collections from there. Two of these are

of *Diplobunops* and the others are of *Protoreodon*, *Malaquiferus*, and *Eomoropus*. It is particularly noteworthy that although often much fractured, the remains show almost no distortion, a condition unusual in collections of Eocene age, particularly those from the Uinta basin. The bone for the most part is a light buff color and the teeth amber to dark brown. The beds themselves do not resemble exposures of the Uinta formation in Utah but much more closely resemble the light gray-green middle Eocene reworked volcanic ash of the Bridger formation in southwest Wyoming. The upper Eocene fossil-bearing beds in the Badwater area have been named the Hendry Ranch member by Mr. Tourtelot and regarded as a part of the Tepee Trail formation. Definition and description of these beds are included in part I of this paper.

THE BADWATER FAUNA

MARSUPIALIA? :

Didelphidae? :

Peratherium?, sp.

LAGOMORPHIA :

Leporidae :

Mytonolagus wyomingensis A. E. Wood

RODENTIA * :

Paramyidae :

Rapamys?, sp.

Sciuravus dubius A. E. Wood

Paramyid indet. (large)

Paramyid indet. (small)

Eomyidae :

Protadjidaumo?, sp.

Cricetidae :

Cricetid indet.

CARNIVORA :

Limnocyonidae :

Limnocyon?, sp.

Miacidae :

Miacis, cf. *robustus* (Peterson)

CONDYLARTHA :

Hyopsodontidae :

Hyopsodus, cf. *uintensis* Osborn

PERISSODACTYLA :

Equidae :

Ephippus, cf. *gracilis* (Marsh)

Ephippus, cf. *parvus* Granger

Brontotheriidae :

Brontotheriid indet.

Chalicotheriidae :

Eomoropus anarsius, new species

Helaletidae:

Desmatotherium woodi, new species*Dilophodon*, cf. *leotanus* (Peterson)

Hyracodontidae:

Epitriplopus?, sp.

Aminodontidae*:

Aminodon advenus (Marsh)

ARTIODACTYLA:

Dichobunidae:

Pentacemylus?, sp.*Apriculus praeteritus*, new genus and species

Agriochoeridae:

Protoreodon, cf. *petersoni* Gazin*Protoreodon*, near *P. pumilus* (Marsh)*Protoreodon pearcei*, new species*Diplobunops*, cf. *matthewi* Peterson

Oromerycidae:

Malaquiferus tourteloti Gazin

Leptomerycidae:

Leptotragulus, cf. *medius* Peterson*Leptoreodon?*, sp.

* Rodents are as described by A. E. Wood from material in the collections at Amherst College and not represented in collections at the U. S. National Museum. The *Aminodon* material is that identified by H. E. Wood, II, in the collection of Wood, Seton and Hares.

CORRELATION AND AGE OF THE FAUNA

The fauna listed above is, of course, by present standards upper Eocene in age. Moreover, there would seem to be no doubt but that it is Uintan. Apparently not any of the forms here recognized are characteristically or exclusively Duchesnean. The general association of forms seen in the assemblage and the development reached in certain groups such as the agriochoerids rather strongly suggest an upper Uintan stage close to that at Myton pocket.

Considering first the reasons for not regarding the fauna as Duchesnean, only the rodent which A. E. Wood (1949) cited as questionably *Protadjidaumo* might be interpreted as this age. Nevertheless, this form is also older than Lapoint in age, as Kay (1953, p. 24) cites it as occurring in the Randlett fauna, and the latter I regard as but scarcely distinct from that of Myton, including it ² (Gazin, 1955, chart 1) in the Uintan. The remainder of the fauna is composed of genera that so far as Duchesnean is concerned are characteristically earlier or common to both Uintan and Duchesnean. Thus, besides

² As currently being proposed by the Committee on Nomenclature and Correlation of North American Continental Tertiary of the Society of Vertebrate Paleontology.

Protadjidaumo, only *Epihippus*, *Amynodon*, and *Protoreodon* are common to the two, and the genera *Mytonolagus*, *Rapamys*, *Eomoropus*, *Epitriplopus*, *Pentacemylus*, *Diplobunops*, *Leptotragulus*, *Lep-toreodon*, and possibly *Desmatotherium* and *Dilophodon* are characteristic of the Uintan. Some of these almost certainly gave rise to later types in the Oligocene but the genera in the latter group are not actually known in Duchesnean time. The genera *Sciuravus*, *Limnocyon*, and *Hyopsodus* are survivals from Bridgerian time and *Miacis* ranges through most of the Eocene.

The evidence for regarding the fauna as upper rather than lower Uintan pertains to the presence of *Mytonolagus*, the possible *Protadjidaumo*, and particularly to the stage of development shown in the *Protoreodon* and *Diplobunops* material. On the other hand, the presence of *Sciuravus* (doubtfully this genus according to Wood), *Limnocyon*, and *Eomoropus* might suggest an earlier horizon, but these are comparatively rare forms in Uintan deposits and their absence heretofore in beds as late as Uinta C is not nearly so significant as the fact that the agriochoerids are distinctly advanced over those of Uinta B time.

Question as to whether the Badwater fauna should be correlated with that from Myton pocket or with that known from the Randlett member may well have little significance. *Protadjidaumo* is not known from Myton pocket but the Badwater specimens are stated by A. E. Wood to consist of incisors only, so can scarcely merit serious debate. *Mytonolagus* is known from both levels but the Badwater form is a different species. *Dilophodon* ("Heteralestes") might suggest a relationship to the Randlett, but Uinta collections in the U. S. National Museum show that this form is present also in the Myton fauna. A slight evidence favoring the Myton fauna is seen in the artiodactyl species represented. Of the Badwater forms, *Protoreodon pumilus* is evidently present in all three occurrences, but *P. petersoni* and probably *P. pearcei* are known only in the Myton fauna. Also, the *Diplobunops* from Badwater resembles the Uinta form *D. matthewi* more closely than it does the broad-skulled *D. crassus*. It is entirely possible that, although a difference in stratigraphic level has been described for the Myton pocket and Randlett occurrences, the differences that may be pointed out are of ecologic significance, as suggested by the rather different nature of the deposits. The beds at the Myton pocket and Randlett occurrences received sedimentary materials from quite different rock sources. I have been unable to detect any change which can be regarded as evolutionary between forms common to the two levels.

Lack of uniformity of opinion regarding the source of Douglass's Eocene materials from the Sage Creek areas makes comparison with the fauna or faunas represented there decidedly unsatisfactory. I have not had the opportunity of studying the field occurrence firsthand so am unable to contribute any information to the stratigraphic picture. Nevertheless, from the materials that I have examined in the collections of Kay and of Hough, understood to be from a single horizon in the Eocene sequence, I find a comparatively close relationship between their fauna and the Badwater assemblage. While I do not concur in several of the identifications cited in Hough's (1955) paper, nor do I agree with the Duchesnean age assignment, there would appear to be a near equivalence in time, possibly also in environment, considering the similarity in faunal representation. With regard to the Douglass collection, I have seen only the helaetid and am reasonably convinced that it represents an advanced dilophodont distinct from the *Dilophodon* in Kay's collection. If, as Horace E. Wood (1934, p. 255) postulates, Douglass's amynodont might have weathered from the overlying Cook Ranch Oligocene, it is not impossible that the dilophodont did likewise and is a distinctly small and perhaps unprogressive species of *Protapirus*. In any case, its stage of development in the line of true tapirs postulated elsewhere in this paper would appear to be later than Uinta B. Recognition of the amynodont remains as *Amynodon advenus* by Wood in both the Douglass and Badwater collections would suggest a near equivalence in time. As to *Hyrachyus douglassi*, it would not appear to be as late as upper Uintan. *H. douglassi* and *Chasmothereoides*, cf. *intermedius* may well be Uinta B, or even earlier.

There remains consideration of the faunas from the Swift Current Creek beds of Saskatchewan and the Tapo Ranch horizon of the Sespe in California. Although the collections known from the Swift Current Creek beds consist of decidedly fragmentary materials there is suggestion of an age which might not be far removed from that at Badwater. Contributing to this is the association of lagomorph and *Hyopsodus* seen in both assemblages.

Of the horizons represented in the Sespe sequence, the Badwater would appear to be nearest to that represented at Tapo Ranch or C.I.T. locality 180. Although the species and most of the genera are not the same, the ages are probably not too different. The distinctive nature of the Tapo Ranch fauna may be largely due to its geographic remoteness.

SYSTEMATIC DESCRIPTION OF THE MAMMALIA

MARSUPIALIA?

DIDELPHIDAE?

PERATHERIUM?, sp.

The isolated lower molar, Amherst No. 10019, which A. E. Wood (1949) regarded as questionably representing *Metacodon* does not seem to me to be insectivore. His careful drawing of this tooth suggests possibly a closer relationship to the marsupials. I am particularly impressed by the lingual position of the hypoconulid, and the posterior deflection of the crest on which this cusp is located, away from the entoconid. The talonid appears to be quite different from the structure seen in *Ictops* and is unlike that, for example, in M_2 of *Metacodon mellingeri* where the hypoconulid is closely connected to the entoconid. For these reasons I have tentatively assigned this specimen to *Pera-therium?*, sp.

LAGOMORPHA

LEPORIDAE

MYTONOLAGUS WYOMINGENSIS Wood, 1949

Plate 1, figure 1

A. E. Wood (1949) has described several isolated teeth of *Mytonolagus* from the Badwater area and a comparatively unworn P^3 was designated the type of *Mytonolagus wyomingensis*. A right maxilla (U.S.N.M. No. 21090) with P^3 - M^2 collected by F. L. Pearce undoubtedly represents the same species. P^3 in this specimen, however, is more worn than in the type, although the teeth in general appear to be less worn than in the type of *Mytonolagus petersoni* which Burke (1934) described from Uinta C at Myton pocket. The teeth are strikingly like those in the type of *M. petersoni*, but it is noted that the hypostriae on M_2 and particularly M_1 are more persistent, extending nearly to the upper limit of the enamel lingually. The comparative weakness of the lingual fold toward the root of M^1 in *M. petersoni* was further noted in upper-tooth material of the Myton form in the collections of the National Museum. At least the hypostria extends nowhere near the upper limit of the enamel. Wood has regarded *M. wyomingensis* as perhaps more primitive than *M. petersoni*.

RODENTIA

Description of the known Rodentia in the Badwater fauna has been covered by A. E. Wood (1949). The collection described by him is at Amherst College.

CARNIVORA

LIMNOCYONIDAE

LIMNOCYON?, sp.

A maxillary fragment (U.S.N.M. No. 21088) with only P^4 may represent *Limnocyon*, but this is not certain. The specimen shows the infraorbital foramen immediately above and anterointernal to the anteroexternal root of P^4 , much as observed in *Limnocyon*. The tooth would appear to be a trifle smaller than in *Limnocyon douglassi* to judge by Peterson's (1919) illustration of this form. The Badwater tooth measures 9.6 mm. long by 9.4 transversely to base of enamel on the deuterocone.

MIACIDAE

MIACIS, cf. **ROBUSTUS** (Peterson), 1919

Plate 1, figure 2

A comparatively large miacid is represented by a lower jaw exhibiting the teeth P_4 to M_2 inclusive. *Miacis* would appear to be indicated by the distinctly basined form of the relatively small talonid of M_2 . The talonid of M_1 may likewise have been basined, although most of the superior surface of this portion of the carnassial is damaged so that its precise form is uncertain. It is, nevertheless, as in M_2 , short and decidedly narrower than the trigonid. M_3 is missing, represented by a single alveolus.

From measurements given by Peterson (1919), the type of *Miacis robustus* from the Uinta at Myton pocket is a little larger than the Badwater specimen. Peterson regarded P_4 and M_1 as subequal in size so that P_4 is evidently both relatively and actually larger in the type. This tooth, however, in U.S.N.M. No. 21087 closely resembles that of the type in the presence of a prominent anterior cusp and a strong talonid cusp, followed posteriorly by a well-developed cingulum. The abbreviation of the talonid in both M_1 and M_2 likewise suggests *M. robustus*.

The type of *Miacis uintensis* Osborn (1895) from Uinta B would appear from the scale of Osborn's illustration to be a little shorter

in length of cheek teeth and distinctly shallower jawed than the Badwater form. Moreover, P_4 in the type of Osborn's species apparently lacks the anterior cusp but has one more cusp on the posterior crest, to judge by the illustration (fig. 2), resembling more closely the referred tooth, A.M. No. 1895. M_1 is relatively smaller, and M_2 in Osborn's type has a higher trigonid and a less distinctly basined talonid.

Miacis gracilis Clark (1939) is, of course, a decidedly smaller species and P_4 is evidently characterized by two posterior cusps in addition to the cingulum.

MEASUREMENTS IN MILLIMETERS OF LOWER TEETH
IN *Miacis*, cf. *robustus*, U.S.N.M. NO. 21087

P_4 , anteroposterior diameter : transverse diameter.....	10.5 : 5.4
M_1 , anteroposterior diameter : transverse diameter of trigonid.....	13.0 : 7.5
M_2 , anteroposterior diameter : transverse diameter of trigonid.....	5.6 : 4.3

CONDYLARTHRA

HYOPSODONTIDAE

HYOPSODUS, cf. UINTENSIS Osborn, 1902

Plate 1, figure 3

A single *Hyopsodus* upper molar, U.S.N.M. No. 21089, may well represent *H. uintensis*, although some doubt may be entertained as comparisons involving such limited material cannot be entirely satisfactory. The tooth is about intermediate in size between M^1 and M^2 in the type, A.M. No. 2079, but resembles M^2 more closely than M^1 . The Badwater molar measures 4.3 mm. long by 5.6 transversely. This is too small to occlude properly with the type lower molar of *Hyopsodus fastigatus* Russell and Wickenden (1933) from the Canadian Swift Current Creek beds.

It is interesting to note that although the type, and presumably the two referred lower jaws mentioned by Osborn, are from the Uinta C of Utah, there is in the collections of the U. S. National Museum a lower jaw from Uinta B at White River pocket.

Mention may also be made of an upper Eocene occurrence of *Hyopsodus* at the Beaver Divide. The specimen, an upper molar, comparable in size to the Badwater tooth, was collected by Van Houten in beds he early regarded as representing the Beaver Divide conglomerate. The locality in question is some distance away from the critical Wagonbed Springs section and Van Houten has since doubted³ the

³ Personal communication.

correlation so that the tooth may well have originated in the Uinta equivalent present in the sequence.

PERISSODACTYLA

EQUIDAE

EPIHIPPIUS, cf. GRACILIS (Marsh), 1871

Plate 1, figure 5

The rather scant material representing *Ephippius* was first encountered in the Badwater localities in 1953. A maxillary fragment, U.S.N.M. No. 21092, including P², P³, and part of P⁴ and a single lower molariform tooth, U.S.N.M. No. 21094, possibly M₂, represent an equid approximately the size of *Ephippius gracilis*.

P² in No. 21092 is advanced over *Orohippus* in the development of the lingual portion, but not nearly so molariform as in *Mesohippus*. The anterointernal cusp in this tooth appears weaker than in the type of *Ephippius parvus* as figured by Granger (1908), being scarcely more than a low crest, extending lingually from the lingual surface of the paracone rather than from a position anterior to the paracone. There is no evidence of a mesostyle on P². P³ would appear to be entirely molariform. The second premolar measures 6.7 mm. long by 5.8 transversely.

The lower molar, in comparison with Uintan horses, shows little of diagnostic importance other than size which is close to that of the preserved molar (M₁) in the type of *Ephippius uintensis* (Marsh), placed by both Marsh and Granger in synonymy with *E. gracilis*. The tooth is a little smaller, though scarcely if any more brachydont than *Ephippius (Duchesnehippus) intermedius*. The V-shaped crests of the lower molar, however, are a little less acute than in the Duchesnean horse. The metaconid and metastylid are separate at the apex but this has been noted in molars as well as premolars of both the Uintan and Duchesnean *Ephippius*. The tooth measures 9.0 mm. long by 6.3 wide.

EPIHIPPIUS, cf. PARVUS Granger, 1908

Plate 1, figure 6

The material of a smaller horse in the Badwater fauna likewise includes a maxillary portion with P² and P³, U.S.N.M. No. 21091, and an isolated lower molariform tooth, U.S.N.M. No. 21093. There is, in addition, the greater part of an isolated molariform upper cheek tooth.

P² in the specimen compared with *E. parvus* is distinctly more progressive looking than in No. 21092 believed close to *E. gracilis*. The anterointernal cusp is clearly defined on a crest extending posterolingually from a position anterior to the lingual surface of the paracone, somewhat as it appears in the type of *E. parvus*, but with the long diameter of the cusps directed a little more transversely than in the latter, so that the anterior portion of the tooth seems broader. Moreover, the outer wall shows evidence of an incipient mesostyle, better developed in the type, but no trace of which was found in P² of No. 21092. P² in No. 21091 measures 6.1 mm. long by 5.1 wide transversely; P³ is 6.7 by 6.9.

The lower molariform tooth is quite like that (No. 21094) compared to *E. gracilis* but distinctly smaller. It measures 7.8 mm. long by 6.3 wide, comparing favorably in length, but a little broader than molariform lower teeth in A.M. No. 2066 referred to *E. parvus*.

BRONTOTHERIIDAE

A fragmentary maxillary portion without teeth but showing root portions of the canine and first two premolars would appear to be of a titanotheres. Speculation as to the genus represented would be unwarranted. Enamel fragments of large teeth in the collection may also be titanotheres, but this is uncertain as they might equally well represent an amynodont rhinoceros.

The Badwater specimen cited by Wood, Seton, and Hares (1936) as *Telmatherium*, cf. *cultridens* is half of a lower molar which W. K. Gregory, in a note to Wood, observed, "Granger and I found this tooth to be close to M₂ of referred specimens of *Telmatherium cultridens*." There is, of course, a close resemblance; nevertheless, from the very fragmentary nature of the specimens it is extremely doubtful if among the several genera of Uintan titanotheres all can be excluded from consideration. The specimen from Lysite Mountain identified by G. E. Lewis (in Tourtelot, 1948) as *Telmatherium*, cf. *cultridens* I have not seen. It could not be located in the collections at Yale Peabody Museum.

CHALICOTHERIIDAE

EOMOROPUS ANARSIVUS,⁴ new species

Plate 2, figures 1-3

Type.—Greater part of left side of skull and left ramus of mandible, U.S.N.M. No. 21097.

⁴ *Anarsios* (Gr.), incongruous, strange—in allusion to the large and unexpected canine.

Horizon and locality.—Hendry Ranch member of Tepee Trail formation on Dry Creek, SE $\frac{1}{4}$ sec. 9, near line between secs. 9 and 16, T. 39 N., R. 92 W., Wind River Basin, Wyo.

Specific characters.—Teeth only slightly larger than in *Eomoropus amarorum*, but skull proportions and depth of lower jaw much greater. Parastyle of upper molars increasingly prominent from M¹ to M³, considerably more extended anteroexternally than in *Eomoropus annectens*, and evidently more so than in *E. amarorum*.

Discussion.—One of the more important discoveries in the upper Eocene of the Wind River Basin is the skull and jaw material of the chalicotheres, *Eomoropus*. The specimen (U.S.N.M. No. 21097) consists of the left half of the skull and left ramus of mandible, and was found by F. L. Pearce in exposures on an eastern tributary of the east fork of Dry Creek about 20 miles west of the Badwater Creek localities. The deposits here were mapped by Tourtelot ⁵ as the same formation as that exposed along the south side of Badwater Creek and are believed to be the same age.

The species represented was earlier (Gazin, 1955, p. 77) thought to be *Eomoropus amarorum*, but subsequent direct comparison with the type, A.M. No. 5096, would seem to preclude this possibility. *E. amarorum* was described by Cope (1881) from a specimen consisting of the posterior portion of a skull, a lower jaw, and certain other portions of the skeleton illustrated by Osborn (1913), and derived from the Washakie Basin. According to Osborn, Cope's specimen probably came from near the base of Washakie B, or the upper Washakie. I suspect that the horizon represented is from higher in the Washakie than suggested, inasmuch as *E. amarorum* would appear to be more progressive than Uinta B *Eomoropus annectens*.

Comparison of *Eomoropus anarsius* with the type of *E. amarorum* shows similarities in the orbital region but the depth of the face below the lower margin of the orbit is conspicuously greater, also the post-orbital process of the frontal appears less prominent and overhanging. The lateral view of the squamosal is similar in the two with the relative position of the external auditory meatus with respect to the glenoid surface much the same. However, the distance between the last molar and the glenoid surface is about 30 percent greater in *E. anarsius*. Moreover, the depth of the lower jaw is also nearly 30 percent greater and the masseteric fossa is more deeply impressed and better defined. The two animals would appear to be at about the same stage of maturity, with *E. amarorum* possibly a little older, to judge

⁵ U.S.G.S. Oil and Gas Investigations Map OM 124, sheet 1.

by wear of M_1 (compare height of cusps shown in lateral view, pl. 2, fig. 1, with Osborn's fig. 3A on p. 267, 1913).

Unlike the type of *E. amarorum*, the cranial portion of the *E. anarsius* skull is poorly preserved, but fortunately the side of the rostrum, missing in the former, is present in the Dry Creek specimen. Perhaps the most striking feature to be revealed by the *E. anarsius* rostrum is the enlarged canine, evidently not included in the dentition of *Moropus*. Absence of this tooth has been generally regarded as characterizing the family although in certain forms the complete formula is not known. The upper premolars were not preserved in

MEASUREMENTS IN MILLIMETERS OF DENTITION IN TYPE OF
Eomoropus anarsius, U.S.N.M. NO. 21097

Length of upper molar series, M^1 - M^3 inclusive, parallel to tooth row.....	54.4
M_1 , anteroposterior diameter perpendicular to anterior margin.....	14.9
M_1 , greatest transverse diameter across parastyle and protocone.....	16.7
M_2 , anteroposterior diameter perpendicular to anterior margin.....	19.0
M_2 , greatest transverse diameter across parastyle and protocone.....	23.5 ^a
M_3 , anteroposterior diameter perpendicular to anterior margin.....	19.6
M_3 , greatest transverse diameter across parastyle and protocone.....	25.0
Length of preserved lower cheek tooth series, P_3 - M_3 , inclusive.....	78.0
Length of lower premolars, P_3 - P_4	24.0
Length of lower molars, M_1 - M_3	54.0
P_3 , anteroposterior diameter: transverse diameter of talonid.....	12.8:7.8
P_4 , anteroposterior diameter: transverse diameter of talonid.....	11.2:8.1
M_1 , anteroposterior diameter: transverse diameter of talonid.....	13.9:9.0
M_2 , anteroposterior diameter: transverse diameter of trigonid.....	16.9:10.5
M_3 , anteroposterior diameter: transverse diameter of talonid.....	24.0:10.5

^a Approximate.

No. 21097, but the three molars are complete. *Eomoropus* upper molars are characterized by a lophoid protocone and hypocone, more elongate than in *Moropus*, and with a distinct protoconule. The external wall exhibits a strikingly developed parastyle and a prominent, anteroposteriorly compressed mesostyle and paracone rib. The rib on the metacone is weak or wanting. M^3 exhibits a spurlike metacone directed nearly at right angles to the similarly developed mesostyle.

Comparison with upper teeth in Cope's type is limited to the lingual portion of M^3 and no significant differences are observed. Nevertheless, the anteroexternal root for M^2 and M^3 can be observed in Cope's specimen, and its position is not nearly so forward and outward as in *E. anarsius*, suggesting rather less extension of the parastyle in the molars. Comparison with the excellent upper cheek tooth series preserved in the type of *Eomoropus annectens*, which Peterson (1919)

described from the Uinta B horizon, shows that the Dry Creek specimen has molars rather similar, except that the parastyles are strikingly more outstanding and the teeth are about 20 percent larger. Moreover, the rib on the paracone, in keeping with the parastyle, is better developed.

The lower teeth of *E. anarsius* are quite similar to those in *E. amarorum* and about the same size, although the anterior premolars may be relatively a little larger. *E. amarorum* includes all the lower cheek teeth from P_2 to M_3 , inclusive. In No. 21097 only P_2 of this series is missing, although the inner walls of M_2 and M_3 are not complete. As Osborn has shown, these teeth are much like those in *Moropus*; however, in the earlier form P_2 is a relatively larger tooth and M_3 retains a prominent hypoconulid. Moreover, as observed in occlusal view of the Dry Creek specimen, the crista obliqua in all the cheek teeth following P_2 joins the posterior wall of the trigonid somewhat more buccally and lower than in *Moropus*, so that the W-pattern is not so well developed.

HELALETIDAE

Simpson (1945) included the Helaletidae in the Tapiroidea, an arrangement which is distinctly preferable to including it, as Scott (1941) has, in the Rhinoceroidea. Scott, moreover, included the hyrachiids in the Helaletidae, and although there is much to be said for such a grouping, as the hyrachiids are in many ways intermediate between the tapiroids and rhinocerotids and show certain marked resemblances to *Helaletes*, nevertheless the family distinction as the Hyrachiidae within the Rhinoceroidea, as advocated by H. E. Wood, II (1934) and retained by Simpson (1945), may well be more desirable.

The Eocene tapiroids are structurally a comparatively conservative group, distinguished from one another by relatively small and seemingly unimportant differences. Nevertheless, at least two families, the Helaletidae and Isectolophidae, should probably be recognized for North American forms.

DESMATOTHERIUM Scott, 1883

Originally described by Scott as coming from the Bridger Eocene, it is now understood that the type of *Desmatotherium guyotii* came from the Washakie beds (see Granger, 1909, p. 22) and is in all likelihood upper Eocene rather than Bridgerian in age. Peterson (1919, p. 127) was evidently in error in citing the locality for this specimen as "Henry's Fork, Wyoming."

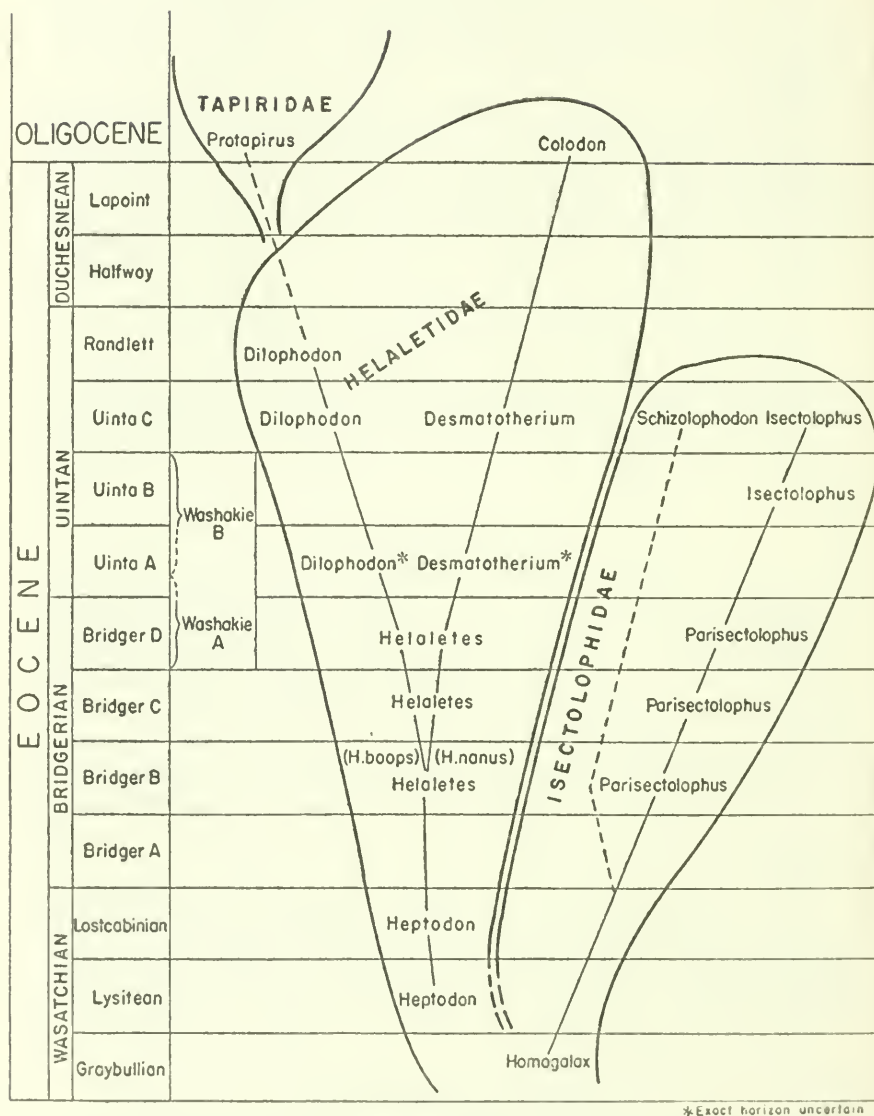


FIG. 1.—Suggested phylogenetic arrangement of North American Eocene tapiroids.

Scott's generic comparisons were made largely with *Hyrachyus*, from which it clearly differs. I am convinced, however, that a distinctly closer relationship to *Helaletes* is indicated. The Badwater, Sage Creek, and Washakie materials together provide the evidence showing the sequence from Bridgerian *Helaletes* through Uintan *Desmatotherium* to Oligocene *Colodon*. As a consequence, *Desmatotherium* should be included in the Helaletidae, as Simpson (1945) has indicated, not with *Hyrachyus* as Peterson (1919) placed it. On the other hand, the subfamily separation of the Colodontinae from the Helaletinae made by Wortman and Earle (1893), which Simpson has preserved, cannot now be reconciled with the sequential arrangement indicated above.

DESMATOTHERIUM WOODI,⁶ new species

Plate 2, figure 4

Type.—Right maxilla with P³-M³ (P⁴ incomplete), U.S.N.M. No. 20200.

Horizon and locality.—Hendry Ranch member of Tepee Trail formation on south side of Badwater Creek, SW cor., SE $\frac{1}{4}$ sec. 14, T. 39 N., R. 89 W., Wind River Basin, Wyo.

Specific characters.—Upper molar teeth approximately 20 percent smaller than in *Desmatotherium guyotii* Scott or *Desmatotherium kayi* Hough. Upper premolars smaller than in these species but relative size intermediate between them and closer to *D. guyotii*.

Discussion.—Four incomplete upper dentitions and a number of isolated teeth, including some from the lower series, all from the Badwater Creek localities, represent the species *D. woodi*. Two of these, part of the type and two upper premolars (part of U.S.N.M. No. 20202) were figured by Hough (1955, pl. 8, figs. 6 and 9) as material referred to the Sage Creek species *D. kayi*. I have examined all the Sage Creek specimens together with the Badwater material and find there is no overlap in observed size range for each. The type of the Sage Creek species is nearly 20 percent larger than that of the Badwater form. *D. kayi* was described as close in size to *D. "guyotii"* but with smaller premolars. The premolars of *D. woodi* are a little smaller than in *D. kayi*, but the ratio of their size to that of the molars is more nearly as in *D. guyotii*.

The principal feature of the upper dentition of *Desmatotherium*, distinguishing it from *Hyrachyus*, is the more progressive condition of the premolars. The divided lingual portion of P³ and P⁴ gives these

⁶ Named for H. E. Wood, II, in appreciation of his work on the Hyrachyidae.

teeth a distinctly more molariform appearance. Resemblance is immediately seen to the earlier *Helaletes nanus* (genotype) which in a similar way is distinguished from *Helaletes boöps*. Washakie *D. guyotii* is a much larger form than *Helaletes nanus*, but *D. woodi* is nearly intermediate. Certain of the larger Bridger individuals with progressive premolars, referred to *H. nanus*, make a close approach to *D. woodi* in size but the separation of the lingual cusps of P^3 and P^4 in any case is clearly not so well effected.

Resemblance of *Desmatotherium* upper teeth to those of *Colodon* is perhaps even more striking; nevertheless, *Colodon* can with little doubt be defended as distinct from *Desmatotherium*. The premolars of *Colodon*, particularly P^2 , would appear to be more progressive and, as shown in illustrations given by Scott (1941, pl. 81) of *Colodon occidentalis*, the posterior upper premolars, noticeably P^3 , would appear to have better defined, more clearly separated, transverse lochs. Moreover, a comparison of measurements shows that although *D. guyotii* is comparable to *Colodon occidentalis* in size, the latter has distinctly wider teeth both in the premolar and molar series. This is perhaps most noticeable in the appearance of the posterior loph of the anterior molars which is decidedly longer in the illustration of *Colodon*.

Lower teeth of *Desmatotherium* are rather poorly represented, except in the Sage Creek collections. They are not known for *D. guyotii* and only certain isolated teeth and tooth fragments are included in the materials of *D. woodi*. Characters of the lower teeth of *D. kayi* were briefly discussed by Hough but somewhat further description, particularly a comparison with the earlier *Helaletes*, seems indicated.

Lower premolars of *Desmatotherium* in comparison with those of *Helaletes* are noticeably shortened anteriorly and relatively broad. Particularly significant is the distinctly larger entoconid which in *Colodon* is quite as large as the hypoconid. There is little evidence for an entoconid in lower premolars of *Hyrachyus*. The progressive development of the entoconid toward *Colodon*, and shortening of the trigonid, give the premolars a more molariform appearance, but the entoconid remains distinct from the hypoconid so that a completely lophoid posterior crest as in the molars is never reached.

The lower molars of *D. kayi*, as in *Helaletes* and unlike *Hyrachyus*, show clear-cut transverse lochs with only a very subdued crista between them, a tooth form already realized in *Heptodon*. The parastylid, particularly on M_3 , seems more reduced in *Desmatotherium* than in *Helaletes* and much more reduced than in *Hyrachyus*. The hypoconulid on M_3 may be slightly more reduced than in either *Helaletes* or *Colodon*. The lower molars of *Colodon*, in addition to

their relatively greater width, are more nearly symmetrical bilaterally, exhibiting a slight crest forward from both the entoconid and metaconid, quite matching those of the labial side.

As previously noted, there seems little doubt but that a phyletic sequence is indicated from *Helaletes* through *Desmatotherium* to

MEASUREMENTS IN MILLIMETERS OF UPPER DENTITIONS
OF *Desmatotherium woodi*

	U.S.N.M. No. 20200 Type	U.S.N.M. No. 20201	U.S.N.M. No. 20202
Length of upper premolar series, P ¹ -P ⁴ , inclusive	33.3
P ¹ , anteroposterior diameter: greatest transverse diameter	7.5: 6.0
P ² , anteroposterior diameter	8.3: —
P ³ , anteroposterior diameter: greatest transverse diameter	9.0: 11.7	8.9: 11.8
P ⁴ , anteroposterior diameter: greatest transverse diameter	8.8: 12.4	9.2: 12.7	9.1: 12.6
			U.S.N.M. No. 20204
Length of upper molar series, parallel to tooth row	37.5
M ₁ , anteroposterior diameter perpendicular to anterior margin	11.0	11.0
M ₁ , transverse diameter across parastyle and protocone	14.0	13.8
M ₂ , anteroposterior diameter perpendicular to anterior margin	12.9	12.8
M ₂ , transverse diameter across parastyle and protocone	15.8	15.0
M ₃ , anteroposterior diameter perpendicular to anterior margin	13.7	13.0
M ₃ , transverse diameter across parastyle and protocone	15.6	15.1

Colodon, and this may logically include *Heptodon* in the lower Eocene which, in addition to a much reduced P₁, has only slightly less progressive premolars than *Helaletes*. The four genera are not readily separated on the basis of molar teeth but a progressive change in the premolars is noted, more precocious in tapiroid character than in contemporary isctolophodont and dilophodont forms (as well as hyrachyid). Nevertheless, this line evidently did not give rise to true tapirs.

DILOPHODON Scott, 1883

Dilophodon was described by Scott (1883) in the same publication as *Desmatotherium* and, as in the case of *D. guyotii*, the type of *Dilophodon minusculus* was attributed to the Bridger Eocene. It is clear that Scott regarded the Washakie beds as Bridger and it is from the Washakie Basin rather than the Bridger Basin, as indicated by Granger (1909, p. 22), that the *D. minusculus* type originated. Granger has the species listed as representing Washakie A, but I suspect that the horizon for this, as well as *D. guyotii*, is B, particularly since both are known from the upper Eocene elsewhere and neither has turned up in the rather extensive collections known from the Bridger proper.

Dilophodon is clearly related to *Heleates* but represents a line separate from that of *Desmatotherium*, possibly derived from the species *Heleates boöps*, having the less progressive premolars or, as seems more than likely, from a somewhat earlier stage. It is not certainly demonstrated that *Dilophodon* gave rise to *Protapirus* but, as far as can be determined, this upper Eocene form possesses all, or nearly all, the requirements in the structure of the teeth that might be sought for in the Eocene ancestor of the true tapirs.

DILOPHODON, cf. LEOTANUS (Peterson), 1931

Plate 1, figures 7, 8

The type of Peterson's *Heteralestes leotanus* from the Randlett locality exhibits beyond doubt an immature dentition so that the characters attributed to the premolar series, particularly the "molariform P₄," apply to the deciduous series, and hence do not serve to distinguish *Heteralestes* from *Dilophodon*.

In the Badwater collection there is a right mandibular ramus (U.S.N.M. No. 20207, figured by Hough, 1955) including all the lower cheek teeth, and both maxillae of a skull (U.S.N.M. No. 21098) with P³-M³ represented, although P⁴, M¹, and M² are not complete. There are in addition almost a dozen isolated teeth or portions of teeth. Comparison between the Badwater and Randlett materials is limited to M₁ and M₂. These teeth in No. 20207 are close in size to those in the type, although possibly a trifle wider, and have similar completely lophoid transverse crests with practically no development of a crista obliqua.

The Badwater form clearly represents a species with smaller teeth than the Washakie *Dilophodon minusculus*, but the lower jaw is deeper and a little more robust. Moreover, the symphysis is broader and ex-

tends posteriorly to a position much farther back than in *D. minusculus*. The width of the lower teeth is not significantly different but those in the Badwater form are a little shorter, particularly in the premolar region. A peculiar parallel with the *Desmatotherium* line is noted in the anteroposterior shortening of the anterior or trigonid portion of the premolars, suggesting that the Badwater form is a little more advanced than *D. minusculus*. This is not an unreasonable suggestion since the Washakie horizon represented by the latter, though possibly earlier than Uinta B, is certainly not later. *D. minusculus* lower teeth, compared in turn with those in *Heleletes*, are seen to resemble them very closely. I note only the somewhat more progressive premolars with distinctly more basined talonids, and the presence of a hypoconulid on M_3 .

Dilophodon leotanus, though having lower premolar trigonids shortened from the *Heleletes* stage, has these portions developed for the most part about as in *Protapirus*, not so abbreviated as in *Colodon*. However, P_2 in the *D. leotanus* specimen at hand is relatively undeveloped. Although this tooth shows characters which are probably variable, the paraconid and metaconid are scarcely more than crests, somewhat as in *Colodon*. Nevertheless, the talonid is more nearly similar to that in *Protapirus* in that the crest of the hypoconid appears to be more median in position as it approaches the trigonid, producing a rather distinctive labial fold or depression.

In the lower molars the parastyle development is rather similar to that of *Protapirus*, although the crosslophs seem more clean-cut.

Significant features are seen in the upper teeth of the Badwater species, and except for M^3 , these teeth were hitherto not known for *Dilophodon*. It may be noted in particular that P^3 and P^4 (P^1 and P^2 are not known) have a single, undivided lingual cusp or deutercone as in *Heleletes boöps*, not divided as in the *Desmatotherium-Colodon* line, and that in M^1 and M^2 the metacone, though exhibiting a heavy cingulum externally, is not concave but distinctly convex labially, so that the metacone has a little more conical appearance. Its form, however, is not quite comparable to that in *Homagalax* or in the middle and upper Eocene isctolophids which, as Hatcher (1896) pointed out, are not entirely suited in this detail as potential ancestors of *Protapirus*. The form of the metacone is unlike *Desmatotherium* or *Colodon* and different than in most of the *Heleletes* material examined, although in some specimens of the latter the concavity is not emphasized and much of the *Heptodon* material would not be excluded as potentially ancestral.

The combination of characters seen in the upper dentition is highly suggestive of *Protapirus* and the possibility of an ancestral relationship is not precluded by the characters of the lower dentition, as it so

MEASUREMENTS IN MILLIMETERS OF DENTITIONS IN SPECIES OF
Dilophodon

	<i>D. minus- culus</i> P.U. No. 10019 Type	<i>D.</i> , cf. <i>leotanus</i> U.S.N.M. No. 20207
Length of lower cheek tooth series, P ₂ -M ₃ inclusive.....	46.6	41.1
Length of lower premolar series, P ₂ -P ₄ inclusive.....	18.7	16.2
Length of lower molar series, M ₁ -M ₃ inclusive.....	28.3	25.4
P ₂ , anteroposterior diameter: greatest transverse diameter	5.6: 3.4	4.8: 3.5
P ₃ , anteroposterior diameter: greatest transverse diameter	6.5: 4.6	5.7: 4.5
P ₄ , anteroposterior diameter: greatest transverse diameter	6.8: 5.5	6.1: 5.2
M ₁ , anteroposterior diameter: transverse diameter of trigonid	8.1: 5.2	7.2: 5.2
M ₂ , anteroposterior diameter: transverse diameter of trigonid	9.4: 5.9	8.8: 6.1
M ₃ , anteroposterior diameter: transverse diameter of trigonid	10.6: 6.3	10.1: 6.5

^e Estimated.

clearly is in the isectolophid line. The phyletic position of *Dilophodon* with respect to *Protapirus* had been suspected by Peterson (1919, p. 113) on the basis of the lower dentition, and the likelihood of such a relationship seems greatly strengthened by information furnished by the upper cheek teeth of *Dilophodon*, cf. *leotanus*.

HYRACODONTIDAE

EPITRIPOLOpus?, sp.

Plate 1, figure 4

A lower jaw fragment with a well-worn cheek tooth, U.S.N.M. No. 21099, evidently a molar, and fragments of two lower molars belonging to another specimen are surely rhinocerotid and would appear to be hyracodont rather than hyrachyid. I am, nevertheless, unable to determine whether the form represented is *Prothyracodon*, *Triplopus*, or *Epitriplopus*. The Badwater teeth are closer in size to those in *Epitriplopus uintense* than they are to those in *Prothyracodon obliquidens*. The teeth also strongly resemble, but are much smaller in size than in the Lapoint hyracodont which Peterson unfortunately named *Mesamynodon medius*. The lower tooth in No. 21099 measures 16.2 mm. long by 11.1 mm. wide.

Dr. H. E. Wood concurs with me that, of the various possible allocations which may be made of this material, *Epitriplopus* is the most probable.

ARTIODACTYLA

DICHOBUNIDAE

PANTACEMYLUS?, sp.

A homacodont that may well be *Pentacemylus* is represented by the posterior two-thirds of M₃. There is no certainty, however, that the form is not *Mytonomeryx*. The tooth conforms closely in form of cusps and is only very slightly smaller than in *Pentacemylus progressus*. It does not appear to represent the smaller *Bunomeryx*.

APRICULUS,⁷ new genus

Type.—*Apriculus praeteritus*, new species.

Generic characters.—Simple conical cusps on upper molars as in *Helohyus*, but these teeth more nearly quadrate with large lingually placed metaconule on all three. Cingulum continuous around molars without external styles and without evidence of a hypocone. Protoconule slightly better defined than in *Helohyus*. P⁴ with single primary cusp and deuterocone.

Discussion.—*Apriculus* is almost certainly a descendant of Bridgerian *Helohyus* and belongs in the Helohyinae, but its trend has been

⁷ *Apriculus*, diminutive of *Aper* (L.), wild boar.

more conservative and along a line independent of that for *Achaenodon*. Change from *Helohyus* has been the increase in size of the metaconule, and the shift to a more lingual position. This is particularly noticeable for M^3 which, rather than having a triangular outline, has achieved the quadrate form of the anterior molars with the metaconule equally well developed. There is, however, no evidence of the development posteriorward of M^3 as in *Perchoerus*; nor do any of the molars show development of a "pseudometaconule" anterolateral to the metaconule.

Distinction from *Achaenodon* is seen not only in the very much smaller size of *Apriculus* so far as known, but in the retention and marked development of the protoconule.

APRICULUS PRAETERITUS,⁸ new species

Plate 3, figure 1

Type.—Right maxilla with P^4 - M^3 (teeth incomplete), U.S.N.M. No. 21100.

Horizon and locality.—Hendry Ranch member of Tepee Trail formation on south side of Badwater Creek, SW cor., SE $\frac{1}{4}$ sec. 14, T. 39 N., R. 89 W., Wind River Basin, Wyo.

Specific characters.—Size of upper molars very close to that for *Helohyus plicodon*. Other differences included in description of genus.

Discussion.—The type maxilla with somewhat damaged upper teeth is the only known specimen of this comparatively late survival of a *Helohyus*-like dichobunid. The upper molars, though comparable in size to those of *Helohyus plicodon*, are perhaps a little narrower transversely, as the basal slope of the protocone and cingulum median to it do not extend so far lingually. The anterointernal and posterointernal portions of the molars are more nearly equal in lingual extent.

Precise measurements of the individual teeth in the type of *Apriculus praeteritus* cannot be obtained because of breakage; nevertheless over-all dimensions can be determined and the length of the preserved portion of the upper cheek tooth series, P^4 - M^3 inclusive, is found to be 30 mm. The molar series is about 24.5 mm. long. M^2 is estimated to be about 8.7 (anteroposteriorly) by 10.6 mm.

In size, upper molars of *Apriculus praeteritus* are only a little larger than the dichobunid tooth figured by Russell and Wickenden (1933).

⁸ *Praeteritus*, overlooked or passed over—overlooked in recent review of collections for upper Eocene artiodactyl study.

The Swift Current Creek⁹ specimen, however, is distinctly less quadrate, and the metaconule, rather than occupying the posterolingual angle of the tooth, is between the protocone and metacone. Moreover, there appears to be a hypocone, or at least a well-developed crest, posterior to the protocone. The structural resemblance of this tooth to both the leptchoerids and diacodexids was noted by Russell and Wickenden. Possibly further evidence bearing on the relationship suggested (Gazin, 1955) for these two groups is to be found in the Swift Current Creek beds when the fauna from there is better known.

Apriculus praeteritus will not be confused with the *Helohyus*?, sp. described by Peterson (1934) from the Lapoint Duchesnean. Although direct comparison in details of teeth is precluded by the different nature of the known material, the disparity in size is alone conclusive, at least as far as species are concerned. The Lapoint specimen, as indicated by Peterson, is rather close in size to *Helohyus lentus*, and although the premolar, disregarding the small parastylid, is rather like that in Bridger *H. lentus*, the molar is not particularly close. The paraconid in M₁, as shown in Peterson's illustration, is much too far forward. *Helohyus* in general does not show the crest extending posteriorly from the protoconid or the triangular-shaped basin formed between this crest and crista obliqua observed in the Lapoint M₁. In *Helohyus* the low crista obliqua extends forward to a much more buccal position on the trigonid, with a well-formed basin posterolingual to this crest.

I strongly suspect that the Lapoint specimen is a very small entelodont. The crest pattern of the molar which Peterson so clearly described and as outlined above, while unlike that of *Helohyus*, can be clearly, though weakly, discerned in unworn first and second lower molars of *Archaeotherium*. In a footnote Peterson called attention to the resemblance of P₄ to that in *Archaeotherium*, but discredited such a relationship by the presence of a paraconid on M₁. This reasoning I cannot understand, as the lingual portion of the trigonid of not too well worn lower molars in the Oligocene form usually shows two

⁹ Omitting consideration of the Saskatchewan Swift Current Creek beds and fauna in my review of upper Eocene artiodactyls was a regrettable oversight and should in no way be regarded as implying a lack of significance. The materials, though fragmentary, give us the only glimpse so far obtained of the nature of the upper Eocene fauna at a latitude so far north. It is only from such Canadian discoveries that speculation by various paleontologists on the possibility of more northern origins of early Tertiary groups with obscure ancestry may be evaluated.

clearly defined and well-separated cusps. Whether the anterior of these originated by twinning or from the cingulum, or whether the two cusps are actually the metaconid and metastylid, would not seem to alter the picture. If subsequent material should demonstrate that the Lapoint specimen is indeed of a small primitive entelodont the possibility of the entelodonts having originated early in the Helohyinae would not seem to be precluded. Although Peterson's specimen is unlike *Helohyus* in details seemingly on a generic level, the bunodont form of the Lapoint molar could possibly be regarded as a modification from that of *Helohyus* or *Lophiohyus*. The interval from Bridger to Lapoint time would seem entirely adequate.

I agree with Peterson that the Lapoint specimen is probably inadequate as a type, nevertheless its possible new-born significance may warrant a name, if for no other purpose than as a handle for discussion purposes. I propose the new name *Dyscritochoerus*¹⁰ *lapointensis*.¹¹ The type is the lower jaw portion described by Peterson, C.M. No. 11912.¹² It might tentatively be aligned with the entelodonts. If *Dyscritochoerus* is in truth a link between the entelodonts and the helohyids its position in the uppermost Eocene is reasonable and would not necessarily imply an Oligocene age for the Lapoint horizon.

AGRIOCHOERIDAE

PROTOREODON, cf. PETERSONI Gazin, 1955

Plate 3, figure 4

Not more than four specimens represent a distinctly small species of *Protorcodon* in the Badwater fauna. Three of these are isolated teeth, but one, U.S.N.M. No. 21101, is a right maxilla including M¹-M³. The teeth correspond closely in size to those in Uinta C *Protorcodon petersoni*, and, like that species, the protoconule is rather weak, not so emphasized as in earlier Uinta C *Protorcodon minor*. The molar series in No. 21101 is 20.0 mm. long.

PROTOREODON, near P. PUMILUS (Marsh), 1875

There are about 18 specimens of a comparatively large form of *Protorcodon*. Most of these are isolated teeth, although a few are jaw or maxillary fragments with two or three teeth, generally broken.

¹⁰ *Dyskritos* (Gr.), hard to determine or doubtful, and *choiros* (Gr.), pig.

¹¹ *lapointensis*, from the town and horizon Lapoint.

¹² Dr. Kay informs me that he has been unable to locate this specimen in the collections at the Carnegie Museum.

These teeth are all of about the size of those in Uintan *P. pumilus*. There is, moreover, no certain evidence that another species such as *Protoreodon primus* is not represented.

PROTOREODON PEARCEI,¹³ new species

Plate 3, figures 7, 8

Type.—Skull, jaws, and other portions of skeleton, U.S.N.M. No. 20305.

Horizon and locality.—Hendry Ranch member of Tepee Trail formation on south side of Badwater Creek, SW $\frac{1}{4}$ sec. 13 near line between sections 13 and 24, T. 39 N., R. 89 W., Wind River Basin, Wyo.

Specific characters.—Larger and more robust than *Protoreodon pumilus*, very close in size to *Diplobunops matthewi*. Marked diastema between canine and P¹.

Discussion.—Although this specimen had been early regarded as *Protoreodon primus* (see Hough, 1955) it is readily distinguished from this species and the advanced *Protoreodon pumilus annexens* by its distinctive size. It is much more easily confused with the equally large *Diplobunops matthewi*. There are several isolated teeth and incomplete dentitions that appear to represent this very large protoreodont, but a number, more fragmentary or too well worn, cannot be allocated as between this form and *Diplobunops*, cf. *matthewi*.

The skull of *Protoreodon pearcei* differs rather noticeably from that of *Diplobunops*, cf. *matthewi* in the Badwater collection (see Gazin, 1955, pls. 10-12) in the anterior extremity of the rostrum. Although the canines are actually larger and as far apart in *P. pearcei*, the snout extremity does not appear so bluntly expanded, evidently because the palate is not so noticeably constricted behind P¹. There is a diastema between the canine and P¹ about the same length as in the *Diplobunops* specimen but there is no diastema behind P¹, and the premolars are distinctly crowded. P² shows a slight basin posterointernally but no deutocone. P³ has a smaller deutocone but a distinctly better defined basin posterointernally than in the *Diplobunops* material, and in P⁴ there is clearer evidence of a tritocone. The upper molars show more lingually sweeping outer crescents and the protoconule may be a little weaker. This is particularly true of M³.

The lower jaw is not so constricted through the symphyseal portion as it is in the *Diplobunops* material figured by Scott (1945, pl. 5, fig.

¹³ Named for Franklin L. Pearce, who found the type specimen.

2). P_1 is a very large caniniform tooth, closely followed by the succeeding, noticeably overlapping premolars. I have not observed significant differences in the lower premolars and molars although from the material at hand the lower cheek teeth of *P. pearcei* are a little narrower than in *D.*, cf. *matthewi*.

Protoreodon pearcei makes a close approach to *Agriochœrus antiquus* in size and in the presence of a short though distinct diastema between the upper canine and P^1 . There is, however, no diastema between P_1 and P_2 . Moreover, the posterior premolars above and below are not nearly so progressive. Also, the protoconule, though very weak on M^3 , is clearly defined on M^1 and M^2 .

I am not certain that this species is represented in Uinta collections, but a robust jaw from Leland Bench Draw with closely crowded premolars and no diastema between P_1 and P_2 may represent *P. pearcei* rather than *Diplobunops matthewi*. Measurements of this jaw were given (Gazin, 1955, p. 64) in comparison with the type materials, showing the shortness of the space occupied by the premolar sequence.

Protoreodon pearcei is apparently represented in the Sage Creek area collections by a skull which has the Carnegie Museum number 8927. It was collected by J. L. Kay in 1940 and the catalog card carries the information "Spring Gulch, Sage Creek." The information "Oligocene (Cook Ranch)" also appears on the label, but this information is surely a misinterpretation of the horizon represented. The skull was figured by Hough (1955, pl. 8, fig. 8) as "*Mesagriochœrus*, cf. *primus*" and the catalog number is incorrectly cited as "9827."

Measurements for the teeth in the type of *P. pearcei* are given with those for *Diplobunops*, cf. *matthewi* in the following section.

DIPLOBUNOPS, cf. MATTHEWI Peterson, 1919

Plate 3, figure 6

In contrast to the rather small ratio of *Diplobunops* to *Protoreodon* specimens encountered in the Uinta basin, *Diplobunops* is almost as abundant in the Badwater collection as *Protoreodon*. Remains of this comparatively large agriochœrid include some of the better preserved materials representative of the fauna and the least distorted known for the genus. Two excellent skulls were collected by Harry A. Tourtelot, one of these, U.S.N.M. No. 20303, has been previously figured (Gazin, 1955, pls. 10-12).

The distinction between *Diplobunops* and *Protoreodon* on the basis of isolated teeth is difficult to make, particularly in the Badwater materials, because with the recognition of the equally large *Pro-*

MEASUREMENTS IN MILLIMETERS OF DENTITIONS IN SPECIMENS OF
Protoreodon pearcei AND *Diplobunops*, CF. *matthewi*

	<i>D., cf. matthewi</i>		<i>P. pearcei</i>
	U.S.N.M. No. 20304	U.S.N.M. No. 20303	U.S.N.M. No. 20305 Type
Length of upper dentition, C (at alveolus)-			
M ³ , inclusive		96.5	90.5
Length of upper dentition, P ¹ -M ³ , inclusive.		83.0	74.0
Upper premolar series, P ¹ -P ⁴ , inclusive.		44.0	36.5
Upper molar series, M ¹ -M ³ , inclusive.	39.5	40.0 ^a	39.6
C, anteroposterior diameter (at alveolus):			
greatest transverse diameter.		7.7: 7.1	11.0: 8.7
P ¹ , anteroposterior diameter: greatest trans-			
verse diameter		9.0: 3.8	7.7: 4.3
P ² , anteroposterior diameter: greatest trans-			
verse diameter	9.6: 5.9	10.3: 6.4	11.1: 6.5 ^a
P ³ , anteroposterior diameter: transverse di-			
ameter *	10.2: 10.2	10.3: 9.8	11.1: 9.5
P ⁴ , anteroposterior diameter: transverse di-			
ameter	10.1: 12.3	10.0: 12.9	10.2: 12.5
M ¹ , anteroposterior diameter: transverse di-			
ameter *	12.8: 15.1	12.0 ^a : —	12.5: 13.5
M ² , anteroposterior diameter: transverse di-			
ameter	13.8: 16.6	13.8: 17.5	13.7: 16.6
M ³ , anteroposterior diameter: transverse di-			
ameter	13.7: 18.0	14.0 ^a : 19.5 ^a	15.0: 18.3
Length of lower cheek tooth series, P ₁ (at			
alveolus)-M ₃ , inclusive			82.5
Length of lower premolar series, P ₁ (at			
alveolus)-P ₄ , inclusive		43.2	38.3
Length of lower molar series, M ₁ -M ₃ , in-			
clusive			44.0
P ₁ , anteroposterior diameter (at alveolus):			
greatest transverse diameter.			10.0: 8.3
P ₂ , anteroposterior diameter: greatest trans-			
verse diameter		10.0: 5.3	9.5: 4.6
P ₃ , anteroposterior diameter: greatest trans-			
verse diameter		11.0: 7.0	10.8: 6.2
P ₄ , anteroposterior diameter: greatest trans-			
verse diameter		12.2: 8.0	11.5: 7.2
M ₁ , anteroposterior diameter: transverse di-			
ameter of talonid.			10.9: 8.1
M ₂ , anteroposterior diameter: transverse di-			
ameter of talonid		14.4: 11.3 ^a	13.0 ^a : 9.3
M ₃ , anteroposterior diameter: transverse di-			
ameter of trigonid.		—: 10.7	20.3: 10.4

^a Approximate.

* Measurements of posterior upper premolars are taken anteroposteriorly across outer portion and transversely perpendicular to outer margin. Those of upper molars are taken anteroposteriorly perpendicular to anterior margin and transversely across anterior portion of tooth, lingually to base of enamel or cingulum.

torcodon pearcei size is no longer an aid. Teeth of *Diplobunops* are slightly less selenodont. The inner and outer crests of the upper molars are seemingly farther apart with the outer cusps a trifle more erect and their apices more buccal or not so lingually directed. The cusps or crests of the lower molars have a slightly more inflated or obtuse look and may be relatively broader. There is, of course, variation in both forms; moreover, these characters of the teeth are scarcely of generic significance and seem somewhat distinctive only between contemporaries in these groups in the higher horizons of Uintan time. *Diplobunops*, so far as known, did not progress much beyond the *Protorcodon* tooth structure characterizing Uinta B time. The genera are, as I have attempted to show earlier (1955), very closely related and their skulls may be distinguished essentially on the different character of the anterior part of the snout.

OROMERYCIDAE

MALAKUIFERUS TOURTELOTI Gazin, 1955

Plate 3, figure 2

The type of this form is from the Dry Creek occurrence some 20 miles to the west of the Badwater Creek localities. Its description and illustration were included in an earlier paper (1955, pl. 16), and need not be repeated here. An isolated oromerycid upper molar (U.S.N.M. No. 21102) in the Badwater collection exhibits the same rectangular form, rugosity, posteriorly bifurcate protocone, and outstanding ribs on the outer cusps as in *Malakuiferous tourteloti*. It corresponds closely in form and size, and in the possession of a slightly outward-deflected metastyle to M^3 . It differs in having a heavier, antero-posteriorly developed mesostyle. The shape of this tooth is entirely different, although structurally related to that in *Oromeryx plicatus*. Likewise, it would not be confused with the comparatively large *Protylopus? annectens*.

This tooth lends support to the belief that the Dry Creek occurrence is probably equivalent in time to that at Badwater, a conclusion earlier reached on the basis of lithology, and the general upper Eocene indication by the presence of *Eomoropus*.

LEPTOMERYCIDAE

LEPTOTRAGULUS, cf. MEDIUS Peterson, 1919

Plate 3, figure 5

Two lower jaw portions, and probably several of the isolated molars, represent a form close or identical to the upper Uintan *Leptotragulus*

medius. One of the jaw portions (U.S.N.M. No. 21104) with P_4 and M_1 falls within the size range of the Myton material, but the other (U.S.N.M. No. 21103), which has P_3 - M_1 , is a little larger than any in the above series. Nevertheless the latter is closer in size of teeth to *L. medius* than it is to *L. proavus*. The structure of the lower premolars in these jaws corresponds very closely to that regarded as characterizing *Leptotragulus*.

The teeth in both Nos. 21103 and 21104 are significantly smaller than in the type of *Leptotragulus? significans* Russell from the Kishenehn beds in British Columbia. Although I have not examined the Kishenehn specimen, from Russell's clear description and stereoscopic illustrations I would favor referring his form to *Leptomeryx* rather than *Leptotragulus*. As a consequence, there would seem to be somewhat better evidence for the Oligocene age postulated by Russell as an alternate possibility for the Canadian occurrence.

LEPTOREODON?, sp.

Plate 3, figure 3

A couple of isolated premolars in the collection, a little smaller than in *Leptoreodon marshi* but not greatly different in size from *Leptotragulus medius*, exhibit a well-defined metaconid. In one of these the metaconid is opposite the protoconid and shows a well-defined groove between them anteriorly, much as in characteristic material of *Leptoreodon*. The parastylid, however, is a well-developed column distinct from the anterior crest of the protoconid, suggestive of *Leptomeryx*. Nevertheless, as in *Leptoreodon* and unlike *Leptomeryx*, the talonid basin is formed by the posteroexternal crest swinging lingually near its posterior extremity, joined only by a weak spur from the metaconid. In *Leptomeryx*, the hypoconid and entoconid in P_4 are in most cases sharply separated and join forward with the protoconid and metaconid respectively. The second isolated P_4 exhibits a parastylid much as in *Leptotragulus*, but the metaconid, though weak, is distinct and unlike *Leptotragulus*. This tooth has a very primitive look and may not represent any known leptotragulids.

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EXPLANATION OF PLATES

PLATE I

LAGOMORPH, CARNIVORE, CONDYLRARTH, AND PERISSODACTYLS FROM
THE BADWATER UPPER EOCENE

- FIG. 1. *Mytonolagus wyomingensis* A. E. Wood: Right maxilla (U.S.N.M. No. 21090), occlusal view of teeth. $4\times$ natural size. Badwater upper Eocene, Wind River Basin, Wyo.
- FIG. 2. *Miacis*, cf. *robustus* (Peterson): Left ramus of mandible (U.S.N.M. No. 21087), occlusal and lateral views. Natural size. Badwater upper Eocene, Wind River Basin, Wyo.
- FIG. 3. *Hyopsodus*, cf. *uintensis* Osborn: Right upper molar (U.S.N.M. No. 21089), occlusal view. $4\times$ natural size. Badwater upper Eocene, Wind River Basin, Wyo.
- FIG. 4. *Epitriplopus?*, sp.: Left lower molar (U.S.N.M. No. 21099), occlusal view. Natural size. Badwater upper Eocene, Wind River Basin, Wyo.
- FIG. 5. *Epihippus*, cf. *gracilis* (Marsh): Right maxilla (U.S.N.M. No. 21092), occlusal view. Twice natural size. Badwater upper Eocene, Wind River Basin, Wyo.
- FIG. 6. *Epihippus*, cf. *parvus* Granger: Right maxilla (U.S.N.M. No. 21091), occlusal view. Twice natural size. Badwater upper Eocene, Wind River Basin, Wyo.
- FIGS. 7, 8. *Dilophodon*, cf. *leotanus* (Peterson): 6, Right upper cheek teeth (U.S.N.M. No. 21098), occlusal view (incomplete P⁴ reversed from left side). 7, Right lower cheek teeth (U.S.N.M. No. 20207), occlusal view. One and one-half times natural size. Badwater upper Eocene, Wind River Basin, Wyo.

PLATE 2

PERISSODACTYLS FROM THE DRY CREEK AND BADWATER UPPER EOCENE

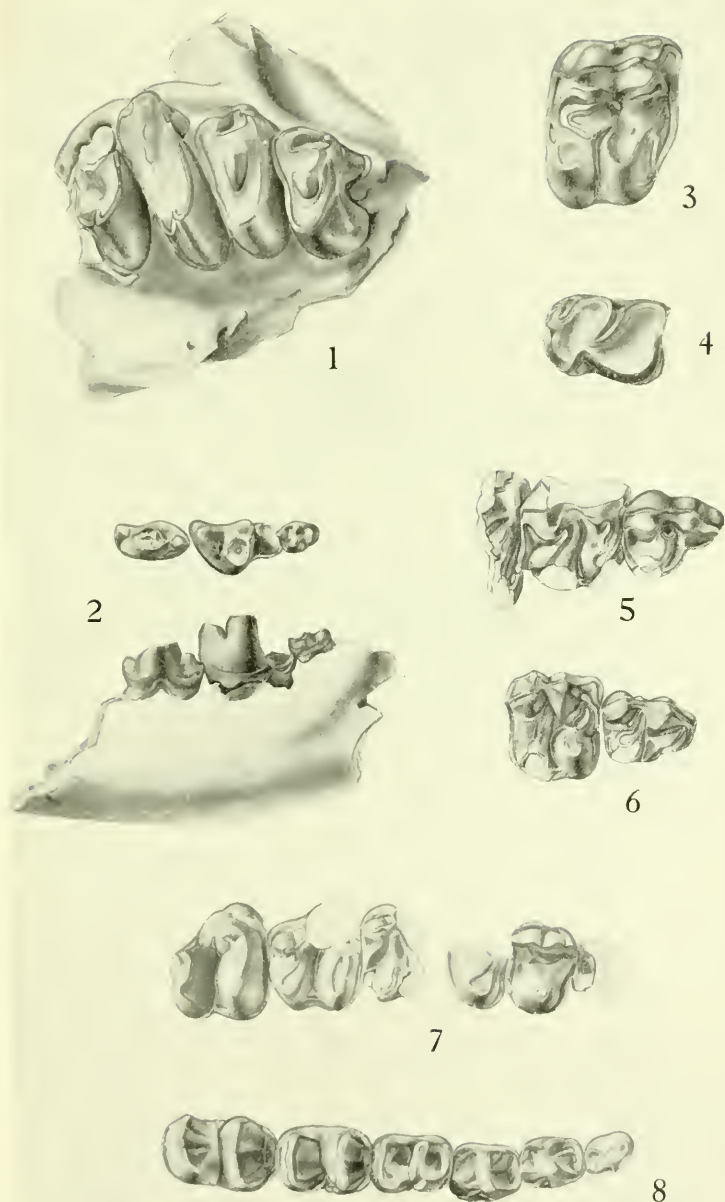
- FIGS. 1-3. *Eomoropus anarsius*, new species: 1, Skull and left ramus of mandible (U.S.N.M. No. 21097), type specimen, lateral view. Two-fifths natural size. 2, Left upper molars (U.S.N.M. No. 21097), type specimen, occlusal view. Natural size. 3, Left lower cheek teeth (U.S.N.M. No. 21097), type specimen, occlusal view. Natural size. Dry Creek upper Eocene, Wind River Basin, Wyo.
- FIG. 4. *Desmatotherium woodi*, new species: Composite right upper cheek tooth series; premolars (U.S.N.M. No. 20202), occlusal view; molars (U.S.N.M. No. 20200), type specimen, occlusal view. Natural size. Badwater upper Eocene, Wind River Basin, Wyo.

PLATE 3

ARTIODACTYLS FROM THE BADWATER UPPER EOCENE

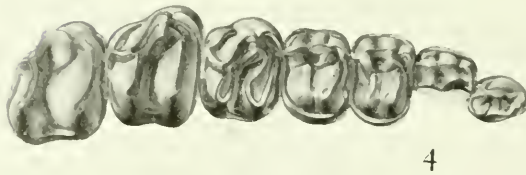
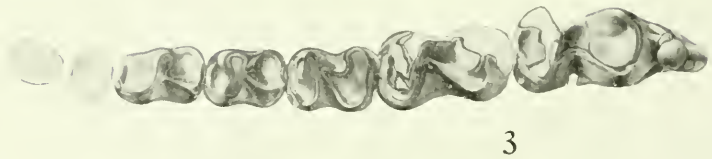
- FIG. 1. *Apriculus procteritus*, new genus and species: Right maxilla (U.S.N.M. No. 21100), type specimen, occlusal view. Twice natural size. Badwater upper Eocene, Wind River Basin, Wyo.

- FIG. 2. *Malaquiferus tourteloti* Gazin: Right upper molar (U.S.N.M. No. 21102), occlusal view. Twice natural size. Badwater upper Eocene, Wind River Basin, Wyo.
- FIG. 3. *Leptoreodon?*, sp.: Left P_4 (U.S.N.M. No. 21105), occlusal view. Twice natural size. Badwater upper Eocene, Wind River Basin, Wyo.
- FIG. 4. *Protoreodon*, cf. *petersoni* Gazin: Right maxilla (U.S.N.M. No. 21101), occlusal view. Twice natural size. Badwater upper Eocene, Wind River Basin, Wyo.
- FIG. 5. *Leptotragulus*, cf. *medius* Peterson: Right ramus of mandible (U.S.N.M. No. 21103), occlusal and lateral views. Twice natural size and natural size, respectively. Badwater upper Eocene, Wind River Basin, Wyo.
- FIG. 6. *Diplobunops*, cf. *matthewi* Peterson: Right upper cheek tooth series (U.S.N.M. No. 20304), occlusal view (P^2 and P^3 restored from left side). Natural size. Badwater upper Eocene, Wind River Basin, Wyo.
- FIGS. 7, 8. *Protoreodon pearcei*, new species: 7, Right upper cheek teeth (U.S.N.M. No. 20305), type specimen, occlusal view. Natural size. 8, Right lower cheek teeth (U.S.N.M. No. 20305), type specimen, occlusal view (P_1 reversed from left side). Natural size, Badwater upper Eocene, Wind River Basin, Wyo.

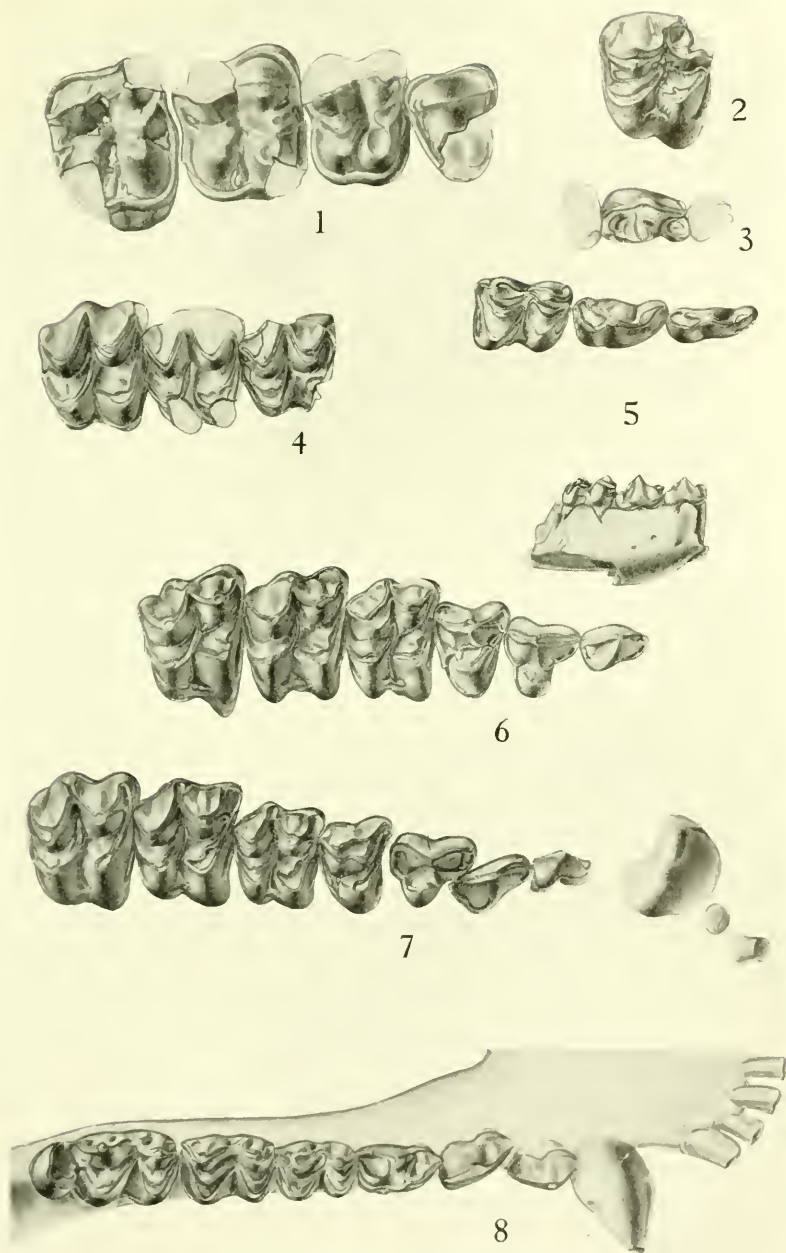


LAGOMORPH, CARNIVORE, CONDYLRARTH, AND PERISSODACTYLS FROM
THE BADWATER UPPER EOCENE

(See explanation of plates at end of text.)



PERISSODACTYLS FROM THE DRY CREEK AND BADWATER UPPER EOCENE
(See explanation of plates at end of text.)



ARTIODACTYLS FROM THE BADWATER UPPER EOCENE
(See explanation of plates at end of text.)



SMITHSONIAN MISCELLANEOUS COLLECTIONS
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BREEDING AND OTHER HABITS OF CASQUED
HORN BILLS (*BYCANISTES SUBCYLINDRICUS*)

(WITH 6 PLATES)

By
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PREFACE

I went to Uganda at the invitation of the East African High Commission to carry on virus research as a visiting scientist at the Virus Research Institute, Entebbe, where I worked from August 1954 until mid-May 1955. My ornithological observations were made as an amateur in the early mornings and evenings, and on weekends. It had been my hope to study some particular field problem in addition to making a general acquaintance with African bird life. The nature of the problem was determined soon after my arrival. In my bird notes, black-and-white casqued hornbills [*Bycanistes subcylindricus* (Sclater)] soon took up more pages than any other species. They came to our garden frequently. In addition, a pair of them roosted and carried on courtship activities in a tree above our house. When I discovered a concentration of hornbill nests in the Mpanga Research Forest, it was apparent that I had an unusual opportunity to study the natural history of casqued hornbills. Present studies did not begin until many females were already walled in. A few pairs of late-nesting hornbills, however, enabled me to witness the beginning stages of nesting activity. Observations on 16 nesting pairs gave, in the aggregate, a rounded picture of breeding and other habits of these birds. As far as I am aware, this is the first detailed description published on the natural history of *Bycanistes subcylindricus*. Moreau (1936), however, has written of a related species, *Bycanistes brevis*. His account is based on the histories of two nests that he observed in Usambara, Tanganyika.

Acknowledgments.—The writer is grateful to the following individuals for help contributed in various ways: Dr. A. J. Haddow, director, and Dr. W. H. R. Lumsden, assistant director, of the East African Virus Research Institute; H. C. Dawkins, ecologist, Uganda Forest Department; Charles Sandison, curator, Botanical Gardens, Entebbe, for identification of fruits and seeds; Dr. V. G. L. Van Someren, Ngong, Kenya, for identifying insect remains; and Dr. Herbert Friedmann, curator, division of birds, U. S. National Museum, for aid and encouragement in preparation of the manuscript. Two sketches of hornbills by their nests were contributed by my wife, Jane Kilham. The avian scientific nomenclature used is that given by Mackworth-Praed and Grant, 1952.

L. K.

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BREEDING AND OTHER HABITS OF CASQUED HORNBILL (BYCANISTES SUBCYLINDRICUS)

BY LAWRENCE KILHAM

Bethesda, Md.

(WITH 6 PLATES)

INTRODUCTION

Description of area.—Casqued hornbills were studied in an area extending from Entebbe, Uganda, to the Mpanga Research Forest located 13 miles to the west. This area is situated on the north flank of Lake Victoria. It is a few miles north of the Equator, at an altitude of approximately 3,750 feet. The rainfall is about 50 inches a year, with a peak in November and a peak of heavier rains in April. Temperatures vary little from a range of 60° to 85° F. Entebbe is the administrative center of British Government and is beautifully situated on a peninsula in Lake Victoria. Its extensive gardens and natural features make it attractive to an incredibly rich bird fauna. There are few trees, however, large enough for nesting hornbills. The Botanical Gardens have a small patch of forest where a single pair nested.

Eastern Uganda consists principally of rolling hills covered with small native farms or shambas. Excellent climate and abundant rainfall enable natives to raise crops continuously and in wide variety, including bananas, coffee, sugarcane, cotton, and cassava. Small fingers of forest persist along bays of the lake and swampy valleys. Zika Forest, 7 miles from Entebbe, is somewhat more extensive and consists of medium-sized trees. Most of these forest patches are under attacks from natives. Africans are continually collecting firewood or trying to enlarge their shambas. The Mpanga Research Forest was the only place I visited with any concentration of large trees furnishing suitable nesting sites. In a sense it is an island, preserved from encroachment of the ever increasing native shambas. The forest is largely second growth. Some of its trees, however, are 150 feet in height. A network of well-kept trails enabled me to move

rapidly and quietly from one nest tree to another. Most of the nest trees I discovered were within a quarter mile of the headquarters clearing. There were undoubtedly more at a greater distance. The forest covers 1.75 square miles and is $2\frac{1}{2}$ miles long. An African ranger and his assistants who lived at the headquarters clearing (pl. 1, fig. 1) were most helpful in putting up ladders and erecting scaffolds.

Life in Mpanga Forest.—A remarkable feature of the tropical forest was that during many hours I saw and heard few living things, whether I was sitting or moving quietly about. Throughout the day, especially in the first part of the nesting season, casqued hornbills were noisy and conspicuous. Other wildlife activity reached a crescendo early in the morning and again late in the afternoon, set off by the screaming of gray parrots (*Psittacus erithacus*). Great blue turacos (*Corythaeola cristata*) often came to feed on fruit of the same trees as the casqued hornbills. Their rolling calls were tremendous in volume. On the other hand black-billed turacos (*Tauraco schiittii*), running squirrel-like along high branches, were quiet and difficult to find. Two other, smaller hornbills (*Tockus alboterminatus* and *Tockus fasciatus*) occasionally came through the forest in small groups. I never saw or heard an owl at Mpanga. Hawks and eagles were not frequent, but they raised a commotion among hornbills whenever they appeared. Most magnificent was the crowned hawk eagle (*Stephanoaëtus coronatus*). The harrier hawk (*Polyboroides typus*), somewhat vulturine in appearance, would search crevices and holes of dead trees for birds' nests and other prey. Lastly, I encountered the great sparrow hawk (*Accipiter melanoleucus*) for some weeks in the hornbill area. It made a continual shrill call, "ker-kee-kee." I had a strong suspicion, but could not prove, that this powerful bird sometimes preyed on casqued hornbills. Smaller birds were rather retiring. It usually took some searching to see such birds as the West African nicator (*Nicator chloris*), the yellowbill (*Ceuthmochares aereus*), and Narina's trogon (*Apaloderma narina*). Among mammals, troops of redbell monkeys (*Cercopithecus ascanius schmidtii*) were much in evidence at the extremes of the day.

METHODS

Finding nests.—Knowledge of hornbill habits facilitated the finding of nests. The various ways in which 16 nests were located, with the number of nests discovered by each method, may be summarized as follows: Search for the largest tree in an area where hornbills were suspected of nesting (5 nests); chance observation of a male at the

nest hole (3 nests); hearing the feeding chuckle of the male and following it through the forest (2 nests); rattle of female bill in nest opening (1 nest); shrill screaming of female hornbill from behind wall when her nest was approached by foreign hornbills (1 nest); commotion of a group of hornbills surrounding an eagle (1 nest). Two other methods involved observations of a male bird: When on a direct, purposeful flight into the forest (1 nest); and following a bird after it picked up dirt from the ground (1 nest). Finally, one nest located in the Botanical Gardens was first noted by other observers. A helpful clue in finding an actual nest tree, once the general territory had been localized, was the presence of the elliptical stones of *Canarium schweinfurthii* on the ground. This fruit is a main item of hornbill diet. Feces were of little help as signs. They are mostly brown in color, disintegrate rapidly on vegetation, and are expelled away from the nest.

Identification of individuals.—Adult hornbills, as well as young emerging from the nest, have the same pattern of black and white plumage. Males, however, are readily distinguishable from females. As adults they are a third larger and have the huge, forward-projecting casque on the upper bill. Young males, even at time of nest leaving (pl. 1, fig. 2), have a larger bill than adult females. There is an ivory-white patch at the base of the upper mandible. As illustrated by my young hornbill (pl. 2, fig. 1), this patch is very large and is well supplied with blood vessels. It is probably an area of growth. In adult males it is smaller, but can be seen at a distance and, owing to variations in size and configuration, it proved to be of considerable value in recognition of individual birds. It is unknown at what age a young male develops a forward projection of his casque.

Watching hornbills.—Observations on nesting hornbills were made from the ground close to nest trees, using 8 x 50 Zeiss binoculars. A few males were shy and rarely seen at the nest. Ordinarily, however, males came to feed their mates if I sat still and waited. A blind was not essential. I usually watched from the spot which gave the best possible view. Along some trails in Mpanga Forest and in the Botanical Gardens the hornbills were accustomed to seeing people passing below. Hornbills were less shy when constructing nests, possibly because of preoccupation with the work. Many nests were inconveniently located. I therefore concentrated my watching on nests most favorably situated. Only one nest was located low enough for construction of a scaffold, reached by ladders tied in place. One could look inside by pointing a flashlight through the aperture. Ob-

servations were all made by myself except in two instances, both of which I was able to check to some extent on a subsequent occasion.

Captive hornbills.—Field studies have been supplemented with observations on four young captive hornbills, three of which were removed from nests when approximately 6 to 7 weeks of age. A male (pl. 2, fig. 1) and a female (pl. 2, fig. 2), named "Mpanga" and "Zika" respectively, were both taken from nests and have lived in my house for a year. This paper does not present full observations on these captive birds. It is hoped to make a more complete study over a number of years.

GENERAL HABITS OF HORNBILLS

Flight.—Casqued hornbills, with large bills and black and white plumage, were conspicuous birds in the vicinity of Entebbe, especially when they flew over open spaces. They were usually in pairs, the male flying about 20 feet in front of the female. Occasionally she took the lead. Their flight was remarkable. There would be a series of wingbeats, then a glide with head and bill held well up. These glides could be without apparent loss of altitude. If a bird was going downhill, as from our hilltop garden toward the lake, a glide might extend 200 or 300 yards. Either phase of flight was noisy. The wingbeats made a "wush, wush" noise and the glide a prolonged "woo-oosh." These noises were helpful, especially in Mpanga Forest, as they enabled me to know, even at some distance, when a male hornbill was returning to his nest.

Roosting.—There were several opportunities within the Institute Compound for observing roosting habits. From August, when we arrived, until October, a pair of hornbills spent every night in a tree in our garden. They would come in with fair regularity at about 6:50 p.m. and sit together for 10 or 15 minutes in the dusk. Then they would separate to roost on individual perches. These perches were at the periphery of the tree where branches were about one inch in diameter. They were about 20 feet apart and 25 feet above the ground. The male always used his own perch and the female hers. In the period of perching together, either one of the two perches might be used. During my first nights at Entebbe, I was mystified by strange noises coming from the tree, not knowing that they came from hornbills. There would be an occasional "woof" or a whacking of bills on bark. By dawn at 6 a.m. noises increased, especially the bill whackings. The hornbills again perched side by side but were in no hurry to leave. They would finally move to other branches of

the tree, then fly off about 6:45 a.m. They thus spent nearly 12 hours roosting. When I returned from a short safari on October 19, I found that the pair had left. I presumed they had started to nest. Unfortunately, I had not discovered at this time that male hornbills can be identified by the white patch on the bill. I had spent many evenings watching the pair and wondered if they would return. Later I had some evidence that the male continued to roost alone in the Institute Compound. This evidence was most suggestive. On the evening of January 19 I heard a familiar bill whacking outside of my window. A male hornbill was roosting on the same male perch observed early in October. He spent only one night. I now recognized, by the white patch on his bill, that he was the same bird I had observed some weeks before roosting in an unusual place just beyond our garden. At night he was perched on a bare limb 20 feet over a driveway. On the nights of January 28 and 29, he was on the same perch, silhouetted against the sky. On the evening of January 31, this hornbill again came to our big tree, alighting first on the female perch, then settling on the male perch. Apparently the lone male alternated roosting places. Although territory among casqued hornbills was not obvious much beyond the vicinity of the nest tree, it would appear possible that the area used for roosting might be more permanent. This situation would be worth further investigation. My captive hornbills, Mpanga and Zika, became extremely nervous at the approach of the evening. This was true even when in a room with artificial illumination. They appeared to have a strong desire to be on a roost they were used to and where they felt secure. Each bird perched on exactly the same place on the roosting pole night after night.

Courtship behavior and the pair bond.—Casqued hornbills remain closely paired the year around, as far as I could determine. Some of their activities prior to nesting appeared to be courtship behavior. The pair of hornbills that roosted in our garden from August to October could be readily observed. They would come flying in about dusk. Soon after they were perched side by side, the male would jerk his head and pop a cherry-sized fruit to his bill tip. Then he would bend over and try to feed the "cherry" to his mate. Usually she would not accept. This never discouraged his efforts. For example, on September 18 he hung his head and with a few slight heaves ejected a "cherry" from his gullet. He held it delicately in the tip of his huge bill as he offered it to his mate. She refused. The male then opened his bill with an upward toss which sent the "cherry" flying back into his throat. In a few minutes he again produced the

fruit and again she refused to take it. She finally touched the "cherry" with her bill. The male then swallowed the fruit for the fourth and last time. Although this "cherry" presentation was observed on six evenings between September 25 and October 5, she accepted only once. On other evenings the ceremony climaxed in a touching of bills. There was never more than a single fruit involved.

Presentation of a piece of bark, a stick, or a leaf was commonly observed during the nesting period. It was almost always the male who did the offering. On one day, November 20, I observed the reverse process. A male perched in Mpanga Forest was joined by his mate who held a large winged insect in her bill. She gave it to him. He then gave it back and she swallowed it. Possibly she simply liked to have things handed over, even if she had to provide the objects herself.

Mutual preening was another late evening activity of the two hornbills in our garden. On September 15, the female sidled up to the male on his perch. Preening now went on for 20 minutes. The male nibbled at the feathers of his mate's head and neck. She appeared to enjoy this attention. Her head moved slowly backward until the occiput rested on her back and her bill pointed upward. The male meanwhile kept nibbling at her exposed throat. Later it was his turn and she went over the feathers of his head and neck. He did not put his head way back as she had. I seldom saw males do this, once being on March 7 in the Botanical Gardens. A pair of hornbills were together for the first time in 4 months. The recently emerged female, in soiled plumage, was perched close to her mate as she nibbled at the feathers of his exposed throat. Mpanga and Zika, my captive hornbills, were preening each other at 3 months of age. Zika has always enjoyed having her throat tickled gently. Even when sitting in my lap, her head has gone way back in the manner of the wild bird which roosted in our garden. Mpanga has often invited preening. He does this by turning the back of his head to Zika, then ruffling up the feathers. In going over each other's feathers, hornbills take special delight in finding small bits of horny material. They may stop to toss these about, small as they are.

Playing with sticks and bill whacking.—Bill whacking was predominantly a male activity. It was usually done after a male had fed his mate on the nest, but might take place on waking up at dawn or most any time of day. The huge bill would resound like a castanet as it was whacked from side to side on a limb. Females scrape their bills on a perch after feeding.

A favorite occupation of resting male hornbills was to toss a stick

in their bills, continually clamping on it to get a fresh grip. On November 20 I saw one knock off a piece of bark and juggle it about until it dropped. He then fell straight from his perch toward the ground and retrieved the bark with surprising agility. On November 29 a male, after much knocking on dead wood, finally broke off a piece 10 inches long. This fell toward the ground and the bird swooped down 50 feet but failed to catch it. My captive hornbills, male and female, would seize a stick or piece of crumpled paper with great gusto. Their clamping and tossing, however, would soon cause them to loose it. They were amazingly quick at catching any piece of food thrown at them, and when placed by a sunny window, they would try to seize bits of floating dust.

Notes and calls.—In addition to noises made by wings in flight and whacking of bills, casqued hornbills made a din with their notes and calls. At times they sounded somewhat like domestic hens. A pair, perched in separate trees, would keep in touch with a series of hoarse "cuk, cuk's." At times they made single notes such as "ugh" or "woof." Most lugubrious noises might come from a male in search of or temporarily separated from a mate. Thus on September 24 I saw a lone male and a nearby pair of hornbills. The single bird made "ka-ka-ka" and "ka-wack, ka-wack, ka-wack" noises of considerable volume. He broke off a small stick, and when he bounced along a limb with it in his bill, the pair flew away at his approach. The male of nest 1 made Mpanga Forest resound with his cries when his mate lost interest in nest building after weeks of futile effort. He was apparently trying to entice her back to the nest hole. Calls associated with nesting were of help in studying hornbills, for I could hear much farther than I could see in the forest. A feeding visit might be announced by a croak when a male came to perch near the nest. Then, when clinging to the entrance and transferring food, males usually made a low, rapid feeding chuckle as bills touched. Females sometimes responded with low guttural notes. These birds, walled within the nests, had a repertoire of their own. Two different noises were made with the bill. The first was a rapid, woodpecker-like tapping made with the tip of the bill, used broadside. Females tapped not only in constructing the original nest wall, but also when walled inside the tree. Sometimes they were repairing the nest wall, but at other times I conjectured that they were tapping on the sides of the hollow tree by way of idle amusement, for the persistence of tapping in some nests was greater than could be expected from repair work alone. My captive hornbills tapped in similar fashion on the walls of their cage when 7 and 8 months old. Two further noises of nesting females

expressed alarm. One was a rattling of the slightly opened bill in the aperture of the mud wall. The bill was visible from the ground. A second alarm noise was a loud, wailing screech. I never heard this call except from a nesting female in distress. Nest 15 was first located by following such screaming through 700 yards of forest. A foreign pair of hornbills was by the nest when I arrived. Such intrusions were a frequent cause of screaming. Similar screams were heard from another female whose mate, early in the nesting season, fed her comparatively infrequently, and from another female whose mate had been recently killed. I seldom heard chirping of the young inside a nest. A newly hatched chick observed in nest 10 made a "chirpee, chirpee" note. Older young ones, as I learned from my captives, can make an assortment of chittery, whistling, and screaming noises. The whistling somewhat resembled that of a smaller species of hornbill, *Tockus fasciatus*.

NEST CONSTRUCTION

Hole hunting.—I first noted nesting activities of hornbills late on the afternoon of October 13. A male flew to the top of a high tree by the lake shore and peered into a hole. He was soon joined by his mate, who took her turn, looking into the hole for 10 minutes. Then she went inside and excavated pieces of rotten wood up to 8 inches long which she tossed out. The male hung his head down to watch what was going on. When his mate finally came out, he started to inspect a second hole nearby. He changed his mind, however, and flew away with a dismal wailing to alight by a hole in another tree. Here he called to his mate with a succession of "caks" and "ughs." He put his head into the hole and pecked at the sides. Within a few minutes his mate joined him. It was apparent from this episode that the male pioneered exploration of possible nesting holes and enticed the female to follow. This observation was borne out by subsequent experience. On November 11, again late in the afternoon, I noticed a male hornbill perched next to a likely looking hole. He flew away and shortly returned with his mate. For the next 5 minutes she kept hanging her head down into the hole and pecking at the entrance. Then she lit on the lower rim, putting head and body inside. When she flew up by the male, he hopped down for another inspection. In Mpanga Forest, I had other examples of the lead taken by the male. Nest 1 had too large an opening for successful nesting. A pair of hornbills spent weeks trying to wall up the aperture, the male's interest persisting longer than that of his mate. On November 7 I found the pair inspect-

ing a hole in a stump 25 feet above ground. I suspected that they were trying to find an alternative to their other nest cavity. They both lit on the rim together, but he kept bending in to remove bits of rotten wood up to 2 inches long. She took a few of these from his bill, but let him continue the excavating. In January I observed further pioneering by a male under unusual circumstances. The male of nest 5 had been killed and his mate had broken out by January 2. I arrived shortly after 9 a.m. To my surprise, I saw a male picking up dirt in the forest clearing. I had seen no signs of nest construction for many weeks. The male's flight led me to the abandoned nest. Here he perched by his mate, then clung to the lower rim of the hole and spent some minutes poking his bill about inside. His mate scrutinized the hole carefully before flying to it. She clung to the rim momentarily, but dropped away as if frightened. This desultory type of inspection went on for 3 weeks. After losing interest in the hole, presumably due to lateness of the season, the pair continued to use the tree as a perch.

Location of nests.—Locations of nests are summarized in table 1. It was apparent that casqued hornbills preferred the largest trees and a hole as far from the ground as possible. Very large trees were scarce, even in Mpanga Forest. Nest 3 was in one of the finest trees (*Antiaris toxicaria*) in the forest, a huge specimen 6 feet in diameter at breast height and possibly 150 feet tall. The large branches supported a growth of epiphytic plants and were draped with lianas. Text figure 1 is a sketch of the nest opening in a limb 85 feet above the ground and shows the male as he always perched preparatory to bending over to feed his mate. Such large trees, free of limbs for 60 or 70 feet, were impossible to climb. Nests were often located where a large limb had broken off, exposing an area of decay. Such a site is illustrated by text figure 2. Plate 3, figure 1, is a photograph of a large tree in the open, showing location of a nest entrance in the stub of a broken branch. Nest 5 was located in a huge arching limb of a *Piptadenia*, as shown in plate 3, figure 2. Some few nests were in less favorable sites. Nest 16, for example, was only 30 feet from the ground in a comparatively small tree. It was relatively easy for an African to climb up and open it. Three nest trees were isolated and in the open and the remainder were in forests. Nest 2 was in a unique position. The cavity was located in a crotch in the top of an exceedingly tall, dead stump. Since the entrance faced vertically upward, one wondered what might happen in a heavy rain storm.

Gathering dirt for building at nest 1.—I learned the most about wall building from a pair of hornbills in Mpanga Forest. Their hole was

TABLE 1.—*Location of nests of Bynasties subcylindricus*

Nest No.	Date discovered	Location	Tree	Location in tree	Height in feet (approx.)	Date found open	Remarks
1.....	10-24-54	Mpanga	<i>Cellis saoyourii</i> Engl.	Trunk	70	—	Unsuccessful nest
2.....	10-24-54	Kisubi	Dead stump	Top	75	—	—
3.....	10-30-54	Mpanga	<i>Antiaris toxicaria</i> (Pers.) Lesch.	Branch	84	1-15-55	Eggshell 11-28-54
4.....	11- 4-54	Mpanga	<i>Cellis zenkerii</i> Engl.	Trunk	50	1- 2-55	Male killed 1-1-55. Female broke out.
5.....	11- 6-54	Botanical Gardens	<i>Piptadenia africana</i> Hook. f.	Branch	70	4- 7-55	Female walled in 119 \pm 2 days
6.....	11-14-54	Mpanga	<i>Cellis zenkerii</i> Engl.	Trunk	75	1-23-55	Eggshell 12-9-54
7.....	11-14-54	Mpanga	<i>Albizia grandibracteata</i> Taub.	Trunk	50	2- 6-55	—
8.....	11-24-54	Near Zika	Unidentified	Branch	54	1-25-55	—
9.....	11-20-54	Mpanga	<i>Antiaris toxicaria</i> (Pers.) Lesch.	Trunk	60	—	Eggshell 11-28-54
10.....	11-21-54	Mpanga	Dead stump	Trunk	30	—	Chick removed 1-22-55
11.....	12- 4-54	Mpanga	<i>Loxoa brownii</i> Sprague	Trunk	85	2- 5-55	—
12.....	12- 4-54	Mpanga	Unidentified	Branch	60	1- 1-55	—
13.....	12- 7-54	Near Entebbe	Unidentified	Trunk	50	1-24-55	Tree in open
14.....	12-17-54	Zika	Unidentified	Branch	45	—	Chick removed 1-21-55
15.....	1-22-55	Mpanga	<i>Antiaris toxicaria</i> (Pers.) Lesch.	Branch	60	—	—
16.....	1-30-55	Mpanga	Unidentified	Trunk	30	—	Chick removed 1-30-55



1. Headquarters clearing, Mpanga Research Forest.



2. Young male hornbill 2 days after emerging from nest 5.



1. "Mpanga," hand-reared male hornbill 10 months of age.



2 "Zika," hand-reared female hornbill 10 months of age.



1. Location (shown by arrow) of nest 13 in stub of broken limb.



2. Nest 5 (location shown by arrows) in *Piptadenia* tree in Botanical Gardens, Entebbe.



1. Termite mound at headquarters clearing, Mpanga Research Forest, where female hornbill collected earth.



2. Entrance of nest 10, showing cement wall.

ideally located. It was 70 feet up in the trunk of a huge tree (*Celtis saoyouxii*), as illustrated by a sketch (text figure 2). Unfortunately the hole was about a foot in diameter and apparently too large. The sketch shows the small wall built across the lower portion. Its rate of construction was exceedingly slow, even though the female worked for

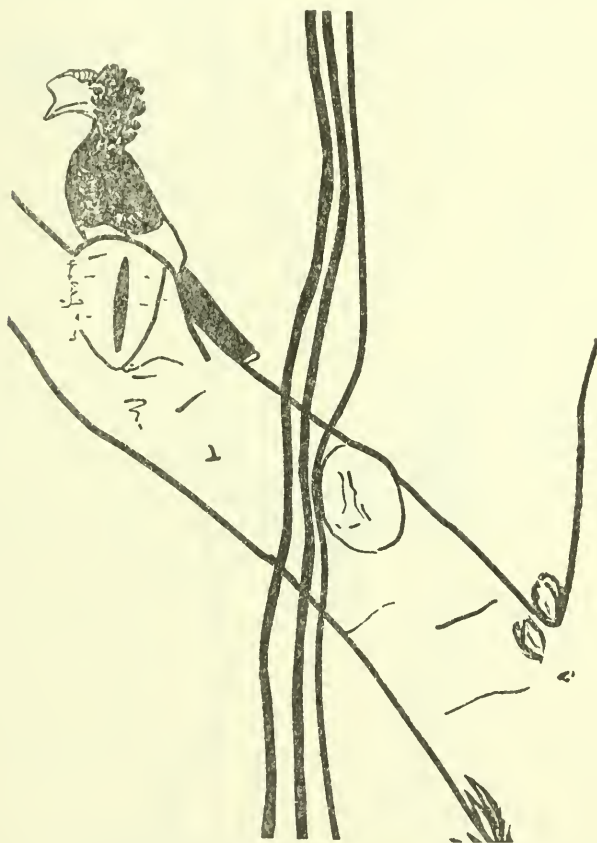


FIG. 1.—Nest 3, Mpanga Forest.

many hours, usually in the morning. On October 24 the pair flew to the hole at 8:45 a.m. The female went inside and the male perched close by. He offered her a mud pellet 5 or 6 times, but she was occupied and paid no attention. At 9 a.m. the male flew to the forest clearing, then down to a path among the shambas. Here he picked two gobs of damp earth, swallowing the first and holding the second, an inch in diameter, in his bill. Then he flew back in stages to the nest tree. I watched him cough up and pass three small mud pellets

to his mate. She took them at her bill tip in rapid succession. The male then remained quietly by for some time while she continued working inside. Twenty minutes later the male again flew to the forest clearing, alighting in a patch of maize. I crept up to within 30 feet and found him perched on a stump several feet above the ground.

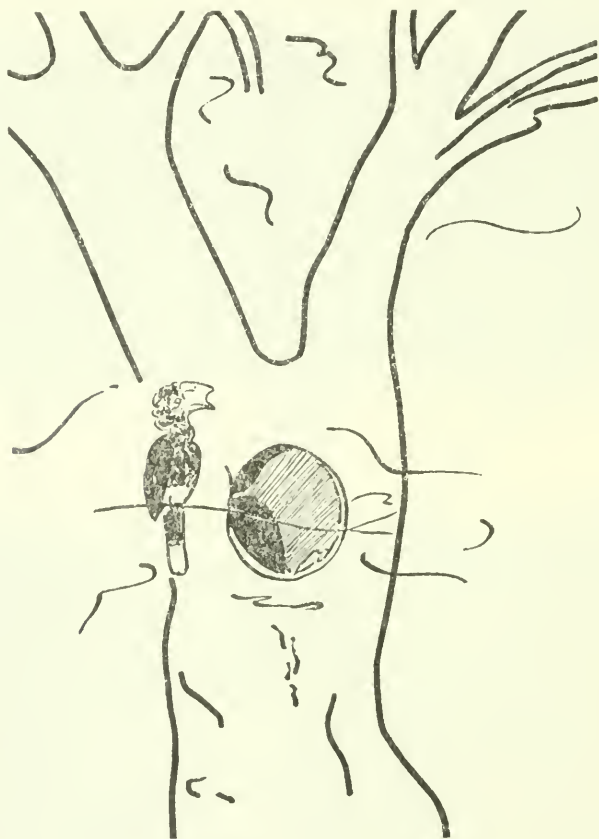


FIG. 2.—Nest 1, Mpanga Forest, never completed.

He was bending over repeatedly, and I could see that he was picking up lumps of earth and swallowing them. To my surprise the female flew over. Both birds now perched together at the forest edge while he coughed up and transferred 5 or 6 pellets to the bill of his mate. Then he hopped away a few feet, broke off a 2-inch piece of bark, and bounced back to offer it to her. She refused it. When the pair had flown into the forest with loud squawking, I examined the stump. A termite nest clung to the side of it. Freshly opened tunnels, now

lined by soldiers, showed where the hornbill had collected earth. On October 27 the male again visited the stump. At 12:30 noon he flew from his nest tree to the maize patch where I was able to observe him from a distance of 25 feet by using a screen of corn stalks. This time he picked up considerable earth from the stump and a little from the ground. Then he flew back to his nest hole, where he spent some time perched on the rim, moving his head about inside where his mate was working. Both birds were silent. So far it appeared that his job was to gather dirt and hers to build with it. However, at 8:20 a.m. on October 31 both birds flew to the forest clearing. She flew to the ground and hopped behind a mud-wattle hut. I moved around to see her bounce up against the wall and knock off a piece of dry mud the size of a plum, which she swallowed. She next hopped around a corner and knocked off another piece. From here she flew up to rejoin her mate. Shortly afterward she followed him to a distant pawpaw tree, where he fed her some fruit. Within 15 minutes they were back at the nest. By 9:10 a.m. the female was working on the nest wall, making a rapid tapping noise like a woodpecker. The male flew away for a short time, apparently to collect dirt. On his return, he perched beside his mate outside the hole, then gave her 11 pellets which she accepted at the tip of her bill and swallowed. She did not use them immediately, for the pair flew away from the nest hole and were gone for a half hour or more.

These observations showed that female hornbills as well as males collect dirt, although they probably do so less often. The female from nest 1 did not always use pellets immediately after swallowing them. Dirt might be retained in her gullet for half an hour or more. The same was true of the male. Since earth was generally hard and dry when collected, the period of retention would give it a chance to become moistened by glandular secretions and by juices from such fruit as paw-paws retained in the gullet at the same time. A larger part of the moistening may be done by the male. I noticed with my captive hornbills that the male could swallow more than twice as much as the female. He is, of course, a third larger in size. It was of interest that hornbills came to termite nests to gather building material, as these nests are exceedingly durable; each grain of earth is selected and coated with a cement substance by the termites. I saw the birds from nest 1 visit a termite nest on another occasion. The pair flew to the edge of the forest clearing at 9:08 a.m. on November 7. The female flew to a low tree, then over the shambas to the tall termite mound shown on plate 4, figure 1. Clinging to its steep sides, she took up 15 chunks of dirt and swallowed them. Finally her mate flew over to

join her. Developments which took place in the next few minutes were unexpected.

Cotition.—The pair had been nest building for at least 2 weeks when they perched together on the termite mound. There was a touching of bills, and the male acted as though he were trying to give her a few extra pellets, but he apparently had none to give. At 9:15 a.m. the female flew from the termite nest, closely followed by the male who made a loud, wailing noise. The two headed toward the nest tree, but lighted on a branch at the forest edge. I had to run across the clearing for a better view. Within this short time the male had mounted the female. He came off a few moments later. Then he mounted on her back again, without hurry, and got securely placed. There was no noise. She had her tail held way over to one side. When he mounted he pressed his tail downward and somewhat under her body. His wings were kept closed. After some moments he got off and flew alone to the rim of the nest. She continued to hold her tail to one side. I could see against a background of white feathers that her vent was extroverted but was retracted shortly afterward. From at least 9:45 a.m. until 12:20 p.m. the female apparently worked from inside the nest on the wall, as she had on previous mornings.

Gathering of dirt at other nests.—At 5 p.m. on November 7 I was watching nest construction by a pair of hornbills in the Botanical Gardens. The male flew toward me and lighted on the ground 35 feet away. Here he picked up 15 or more chunks of earth. After he had flown away, I examined the spot which proved to be a low termite mound. Freshly opened tunnels showed where the bird had been working. Although hornbills appeared to be especially attracted to termite nests they are not invariably so. Sometimes they pick up ordinary dirt. On October 31 the male from nest 4 lighted on a stick close to the ground of a native shamba. He repeatedly bent over, took up chunks of black cultivated soil, and swallowed them. His next move was to an adjacent banana tree. Here he tore off pieces of leaf and bark, 1 to 2 inches long, three of which he swallowed. His subsequent flight to the forest led to the discovery of his nest hole. The wall of this nest was unusually black.

Construction of the nest wall.—At various times I watched four pairs of hornbills constructing their nest walls. There was variation in the time of day when work took place. Three pairs worked in the morning and one pair, from the Botanical Gardens, late in the afternoon. Experience at nest 2 was typical. On October 24, the male returned to his tall, isolated nest stump at noon. He leaned over the nest opening as he heaved up pea-sized pellets of dirt. These he

passed with his bill tip to that of his mate directly below. At least 10 pellets were passed in rapid succession. The male then bounced along to another part of the stump and tried to whack off bits of dead wood. In a few moments he bounced back to the hole. He shook his head from side to side, with bill half open, as though a pellet had gotten stuck. Then for a while he held his head low over the hole to watch what was going on. A week later I found him carrying on much the same. He spent considerable time looking down and even putting his head and neck through the hole. Sometimes his mate accepted two pellets and refused a third. At such periods of active construction, the only sound was the rapid tapping of the female's bill, which could be heard some distance away.

Male hornbills did no work on the walls, although they might peck and explore about a nest entrance. A male usually sat by like a bricklayer's helper. He would fetch building material and supply it to his mate as needed. The pair at nest 1 would spend the larger part of a morning in this fashion, settling down to work at about 8:30 a.m. Work at the Botanical Garden nest was done from midafternoon on. At this time the sun shone directly into the nest entrance. Possibly this pair was taking advantage of the illumination. I could see the female's bill tapping inside. Details of how the tapping was done could not be perceived readily in high nests. I had a better opportunity at nest 7 which was comparatively low. The female was already walled in but on January 29 she was repairing the entrance with material from the nest floor. She applied this material with rapid tapping of the side of her bill tip. Tapping was again seen to good advantage in my captive pair of hornbills. In September 1955, when 9 months of age, both birds would get in a corner of their cage and plaster the wall with any litter, feces, or food matter which might serve as mud. Both sexes did the tapping. This activity was carried on daily, as judged by the appearance of the wall and the amount of tapping we heard.

Abortive nesting.—On November 7, following coition, the pair of hornbills from nest 1 had worked all morning on the nest wall. By the following weekend their interest had obviously declined. The hole was too large to wall in. On the afternoon of November 13 the male kept returning to the nest rim. Then he would fly back to the forest to join his mate. Sometimes the pair would fly together to the nest tree, making a tremendous noise. It was a dismal wailing. The male, however, would look into the nest alone. On the following day I observed the same behavior from 7:15 a.m. until 12:30 p.m. These two were the noisiest hornbills in the forest. It appeared that he was

anxious to continue with the nest, but that she had lost interest, as during the whole morning she never came near it. He would put half of his body inside and make low grunts as he poked about with his bill. The same performance continued on a following weekend. She entered the nest several times, started tapping, then flew out again after a short time. The male persisted for two more weeks in his efforts to have her return. December 4 was the last time I ever saw her in the nest. This was 6 weeks after I had first found her at work. My final view of the pair was on December 12. They were perching near the nest cavity but showed no interest in it.

Structure of wall and the inside of the nest.—Nest entrances were usually elongate slits, $1\frac{1}{2}$ to 2 inches wide and 4 to 10 inches high, depending on the size of the natural cavity. These measurements are approximate. Plate 4, figure 2, a photograph of nest 10, shows a representative nest entrance. Walls were remarkably strong. Neither Africans nor myself, by putting a hand into the slit and pulling hard, could budge or loosen them in three nests opened for removal of young. Much hacking and prying with a curved bush knife were needed to effect an entrance. Another indication of the stoutness of walls was provided at the time of natural nest openings. One-half of the entrance cement of 2 nests (3 and 12) was knocked out entire, apparently by the emerging female. These pieces fell 60 to 85 feet to the ground, where I picked them up unbroken. They were roughly 4 inches long, 3 inches in width and thickness, and were built in concentric layers. Possibly each layer represented a day's work. Odd bits of insects, bark, and plant material were incorporated in the cement in haphazard fashion. In two of the three pieces, one side was dark brown. It did not run with the concentric layers and it had faced the inside of the nest. Females had probably made this addition after being walled in. For lack of earth they had used fruit stones, seeds, and what appeared to be darker fecal material. It did not appear that feces was an integral part of the main cement structure in any of the five nest walls I examined closely.

There was nothing organized about the inside of a nest. Nests 10 and 14, examined at time of opening for removal of young, had fragments of rotten wood at the bottom. Nest 10 also contained many large contour feathers. When I pulled away the cement from this nest, hundreds of small ants swarmed out from behind the edges. My hand and arm were covered with them as I explored the cavity which was roughly a foot in diameter. An African who broke open nest 14 for me had a similar experience. These ants are presumably attracted by feces and other debris, for an amazing amount of fruit

appears to go right through a hornbill's intestinal tract undigested. This is especially true of young birds, as I discovered with my captive specimens. Feces from younger individuals does not always clear the entrance. This was observed from the scaffold by nest 10. There was, therefore, ample organic matter to attract ants, and their presence in great numbers may explain why I failed to find insects, in the nature of parasites, scavengers, or others, in examinations of nest debris.

ACTIVITIES OF NESTING PAIRS

Walling in of female.—As far as I can determine, I was watching nest 5 on the evening when the female began her 4 months of voluntary confinement. On November 7, the male was active late in the afternoon bringing termite earth to his mate, and giving her pellets as she worked. On the following day I arrived at 5:15 p.m. to find him bending over the entrance. The sun shone into the hole. I could see that the nest wall was complete and that no more building was in progress. For the next hour the male stayed close by. At 6:30 p.m. he flew to a large tree (*Canarium schweinfurthii*) and picked some fruit, then returned to his nest with loud wailing. He gave his mate five or six fruits and she made low guttural notes. Dusk was now coming on. The male flew to a limb 15 feet away, then took a long flight which carried him out of sight over the brow of the hill. His mate remained alone. It was not until March 7 that I was to see her again.

Feeding and other attentions of male to mate in nest.—Once walled in the nest, the female was entirely dependent on the male for food until she emerged with her young one some months later. Nest 5 was well situated for observations. I would station myself below the huge *Piptadenia* tree in the Botanical Gardens (pl. 3, fig. 2) every few days during the week, before breakfast and again late in the afternoon. The male was accustomed to people passing beneath the arching limb containing the nest hole. Some days I would wait nearby an hour without seeing him approach the nest. I discovered, however, that there was some regularity to his visits, one usually taking place close to 7:30 a.m. Forty feeding visits were observed in the course of 4 months. A visit on November 13 was typical. At 5:40 p.m. the male came flying over the open lawns, head held high, and wings making a "woo-ooshing" noise. He held a chip of wood 5 inches long in his beak. It looked as though he were flying with a cigar. He landed on the big limb, then bounced sideways until he was on the bole above the nest entrance. Then he leaned over and pushed the

stick of wood through the entrance. When his mate had taken it, he coughed up eight blackish fruits in succession, swinging his head down each time to place them in the tip of her bill. By the time the feeding was done, the stick had come out of the hole. He picked it up and pushed it in again. Then he flew to a perch 15 feet away. At such times he would usually whack his bill loudly back and forth on a limb as one would whet a knife. This male, like most of the others I observed, did not linger in the nest tree after a feeding visit.

Stick or bark presentation was a common prelude to feeding. It occurred in 13 of the 40 visits observed. Objects presented ranged from curled pieces of bark, 1 by 6 inches, to smaller bits an inch in diameter. Discarded and dropped pieces accumulated on the ground below the nest. The male was persistent about these offerings. On December 8 he lighted above the nest and swung his bill down into the entrance 23 times to offer a piece of bark. His mate gave no response. When she accepted on the twenty-fourth try, he fed her four fruits.

The male usually made a feeding chuckle when a fruit was transferred. Numbers of fruits offered varied from 2 to 17 per visit, but counting was often difficult. Thus on February 7 the male fed his mate 17 small fruits. Some of these were offered 4 or 5 times before she accepted. On February 28 he fed her 2 "cherries." A third one, however, had to be held down 11 times before she took it. Possibly the female is at times occupied with the young chick, so that she is not in a position to accept. Fruits brought to the nest ranged from the size of a pea to that of a small plum.

In addition to bringing sticks and fruit, the male of nest 5 cleared away accumulations from the entrance. The approach to the nest, formed by a broken-off limb, sloped slightly upward from the wall. It thus collected fecal and other matter expelled from the nest. The male lingered to clear away this debris after 14 of 40 feeding visits. Sometimes he swallowed a few items. More often he would pick up small bits with his bill and toss them outward in a rapid and systematic fashion. On February 9 he did this 30 times after one visit and on February 28, 25 times. Usually he made only a few tosses before flying away. Nest 7 was the only other nest where I observed a male clearing the entrance.

Observations at other nests, while generally similar to those made in the Botanical Gardens, differed with the individual character of hornbill pairs. Sometimes physical peculiarities of the nest cavity led to differences of behavior. Nest 6 was in the straight trunk of a huge tree and the female often rested with her tail protruding from the



1. Female hornbill at time she was removed from nest 10, approximately two-thirds of the way through nesting period.



2. "Mpanga" and "Zika" when approximately 2 months of age.



1. "Mpanga" at 6 months of age.



2. Young crowned hornbill (*Tockus alboterminatus*).
(Photograph by Dr. Herbert Friedmann.)

entrance. When the male bent over to offer food, she would not always bother to turn around. One day he gave her a fresh green leaf before coughing up four yellow fruits. At nest 12, also at Mpanga, the female would put her whole bill out of the entrance to take food. Possibly females in these last two nests were crowded for space. Some of the holes, such as those of nests 4 and 7, were on straight trunks without boles. Consequently, the visiting males had to cling to the lower rim of the nest with tail fanned out against the trunk. An occasional visiting male would bring bark to his mate but no food.

Expulsion of feces, and other activities of female in nest.—Watching and listening from the ground gave some insight into activities of nesting females. At infrequent intervals one might see a stream of fecal matter shoot 2 to 3 feet out of an entrance hole, glisten in the sun, then land with a splash on the leaves below. The white feathers of the female's rear end were, in some nests, clearly visible as she maneuvered her vent to the opening. Hornbill vents are protrusible and mobile. This could be well seen in our young birds 6 to 8 weeks of age when, standing way up on their legs, they would back up over the edge of the box they were in and expel feces on the floor. Expulsion was not as forceful as seen in some hawks. Tree trunks and foliage below nests were not appreciably stained by expelled feces. This was partly due to the dark color of the droppings resulting from a fruit diet. Some streaking of white appeared in feces with development of the young. On January 8, as I was sitting on the scaffold beside nest 10 in Mpanga Forest, the 4-weeks-old chick backed to the entrance and deposited a cylinder of feces 4 inches long on the lower cement. This feces had a white film over one end. The ladder leading to nest 10 became increasingly spattered with feces as weeks went on. Observations on my captive birds indicate that the white substance in the feces increased with ingestion of animal protein. I saw one nesting female toss debris out of the entrance with her bill. Doubtless this method also contributes to nest sanitation.

Females within the nest did not lose their constructive instincts. Bill tapping continued, but was carried on far more by some females than others. I frequently heard tapping from nests 7 and 10, which were only 120 feet apart, at the same time. Much of the time I could not see a bill in the aperture. It is conceivable that these birds plaster debris against their nest cavities either because habit is strong or just by way of idle amusement. My young captive hornbills plastered the walls of their cage, possibly for the same reasons. Entrance walls, however, sometimes needed repair. On November 28, the female of nest 6 was repairing her nest entrance at noontime. I could see her

bill tapping rapidly on either side of the lower aperture. The shape of this aperture changed somewhat from one week to another and the repaired areas were darker in color. Presumably feces and other debris present by the opening were used, for I later obtained half of the cement from this nest and found that the dark areas had seeds and fruit stones embedded in it.

Nesting females may enlarge their nest cavities by pecking at rotten wood surrounding them. The female of nest 10 had an escape attic above her nest. I could hear her scuttling into it when I climbed up the ladder, and on looking through the opening all I could see was the tip of her tail. When nest 14 was opened on January 21, there was no female in sight. The African who had removed the chick swept the whole length of his arm inside without encountering the mother bird. His position was too precarious for him to look inside. It seemed probable that the mother had crawled into some remote recess.

EGGS, YOUNG, AND NEST OPENINGS

Eggs.—Nest 10 was in a dead tree 30 feet above the ground in Mpanga Forest. On December 4 I climbed the scaffold to this nest for the first time and peered through the aperture, using a flashlight. The mother bird was almost out of sight in her escape attic. There were two white eggs, similar to those of a domestic fowl in size and shape. My next visit was on December 11. The forest ranger said that he had climbed to the nest at 6 a.m. and had seen two eggs. I approached the nest tree at 1:30 p.m. and saw two-thirds of an egg-shell on the ground directly below the nest hole. The shell was so fresh that ants were still swarming over its moist inner surface. I climbed the scaffold to find the mother hornbill facing me at the entrance. This was the only time she ever did so. As far as I could determine before she climbed to her escape attic, she had a complete plumage. When she left I saw one egg and one blind, completely naked, rather blue young one. This was a first view of my subsequent pet, Mpanga. When I looked in on the following morning, I could not see him, but he soon emerged from under some debris, giving a feeble "chirpee, chirpee." His lower bill was larger than the upper one. Early in the morning of December 14 the ranger found the second egg chipped, and by afternoon he saw the shell on the ground and a second chick in the nest. I was able to visit the nest two days later and see the two chicks together. The larger one was chirping lustily. He had brown mash over his bill and throat, and there was more mash in the nest. I wondered whether the mother hornbill had regurgitated food onto the nest floor and then fed it to her offspring.

It was January 1, 1955, before I was able to visit the nest again. There was now a single young one, the size of a plucked pigeon, which begged and peeped a few times when I looked in. The forest ranger reported that the second chick had disappeared a week after hatching. The remaining chick had its eyes open. They were dull but mobile. Pinfeathers were just beginning to emerge on its head and wings. The entrance hole was becoming stained with feces, whereas it had been clean previously. On January 8, the young bird had black pinfeathers one-fourth of an inch long on head, neck, and wings. There were smaller, colorless pinfeathers on back, tail, and in two tracks bordering the breast bone. Feet and an inch-long fleshy tail appeared large for the size of the bird. The chick seized my finger when I pushed it in. He also chewed pieces of wood. This bird was removed from its nest when 6 weeks old and has lived well in captivity for over a year.

Periodic inspections of the ground below nest trees gave clues as to the number of eggs and approximate time of hatching in four other nests. For example, on November 27 I found pieces amounting to two-thirds of an eggshell, with its membranes, below nest 4. I carefully removed all pieces, and on November 28 there were no further eggshells. Six days later, however, I found a second eggshell, three-fifths intact, with an additional one-fifth in pieces. It appeared that two eggs had been laid and that they had probably hatched on different days. This had happened at nest 10. There, it may be recalled, the eggshell was tossed from the nest soon after the hatching of the chick. On the ground below nest 9, I removed most of an eggshell on November 28, and three-fourths of a shell on December 4. These and other data are tabulated in table 1. Data from two other nests were less complete. I found over half of an eggshell below nest 3 on November 28, but it was not until January 1 that a second shell turned up. Possibly it had been covered with debris, either in the nest or on the forest floor. On December 9 there were pieces of one shell below nest 12. I did not, as in the other cases, know how long they had been there.

Breaking open nests to obtain young. Molting of female.—Inaccessibility made it difficult to study the molt in nesting females, but I was able to gather some information. Nest 10 could be reached by ladders. The female was usually in her escape attic and I did not want to interfere with her by making an opening. The nest was well lined by remiges when I looked in on December 4. In retrospect I should have removed them with a pair of long forceps for arrangement and counting. All I could see of the mother bird was her tail. The tail feathers remained soiled with no evidence of renewal. On December 11 I had

my only full view of the mother when she briefly defended her chick. Her plumage appeared complete, but I did not see her outstretched wings. My next view of her was when I broke open the nest on January 22. After putting the 6-weeks-old chick in a bag, I reached into the hollow trunk and pulled the mother bird down. She was kept in captivity for a few days of observation. Plate 5, figure 1, shows that her plumage was complete. The only sign of molting was one tail feather, a few inches long, which was still enclosed in a sheath. She was not shy in captivity, but she remained motionless, as if stunned, and refused to eat. I liberated her on January 24. In spite of a long period of confinement in the nest and having had no food for 2 days, she flew to a tree, squawked a few times, then took a flight of 300 to 400 yards. She was headed back in the direction of Mpanga Forest, 13 miles away.

It was apparent that this female, viewed when roughly one-third, and again at two-thirds through the nesting period, had not experienced any sudden or complete molt. On January 30, we opened nest 16 to remove a chick 6 or 7 weeks of age. The mother bird struggled vigorously, striking the African who held her a sharp blow on the chin, so that he fell over backward. When I took hold of her it was obvious that she was in no weakened condition. Her plumage appeared to be complete except that her tail feathers, although well grown, had sheaths at the base. She flew readily to a tree when liberated.

Premature escape of female due to loss of mate.—When I entered Mpanga Forest on the afternoon of January 1, I heard the wailing screech of a female hornbill in distress. The calls were given twice a minute. I followed them to nest 4 where I found a pair of foreign hornbills. These flew away at my approach. The female in the nest kept screeching for the next 2 hours in a most pitiful manner, but her mate failed to return. I examined the ground below the nest tree and found that he had been killed. There were two large patches of feathers directly below his usual perch. These patches were $2\frac{1}{2}$ to 4 feet across. One consisted principally of small body feathers and the other of large feathers from wings and tail. I suspected that the hornbill had been struck from his perch by some bird of prey, and, after falling directly to the ground, had been plucked on the spot. The female was still screeching when I left the forest late in the afternoon. On the following morning I reached the nest shortly after 9 a.m. The mud wall was partially broken out. A new pair was inspecting the nest and it was evident that the original female was no longer there.

Natural nest openings.—I observed how nests were opened naturally

in five nests with entrances visible from the ground. In each the cement had been knocked away from one side of the aperture. This left ample room for the mother and young to emerge. I was interested to find that the missing cement was lying in an intact piece on the ground below three of the five nests. These five nests (Nos. 3, 6, 11, 12, and 13, table 1) all opened between January 1 and February 5. Some of these may have been open for a week before I noticed them. Nest 6, however, was closed on the afternoon of January 22 but open by 9:15 a.m. on the following day. There were no hornbills in the vicinity.

Emergence of mother and young.—On February 5 I noticed that the female of nest 7, which I had had under observation for 84 days, was still walled in. By the following morning she had left. I began to search the adjacent forest and was able to locate the pair 100 or more feet from the nest tree. The female was recognizable by her soiled plumage, the white patches of which were muddy. The male, recognizable by his bill markings, sat close by her. For the next 2 hours I hunted back and forth through uncut jungle. It was raining hard and I thought that if I could find the young, I could probably catch it if its plumage was water soaked. The parents expressed great alarm, coming down within 20 feet of my head. Unfortunately I could not find the young. I wondered if it had crawled into some hollow limb.

I had better success in the Botanical Gardens. The female was walled in on November 8, 1954, and had emerged with her young one on March 7, 1955. She was confined for 119 days, with a possible error of 2 days. There were no signs of activity by the nest on the morning of March 7. Late in the afternoon, however, I found the male perched by his mate 50 yards from the nest tree. He made continuous noises. Several times he hung his head way back, allowing her to nibble the feathers of his throat. Her plumage was in poor condition. The white parts of her feathers were soiled, her tail ruffled, and the small feathers on the back of her head and neck were worn. There was no sign of the young one. At 7:15 a.m. on March 8 I located the pair by cries coming from a patch of forest. They were together in a tall tree, and a young hornbill was close by. His plumage was in fine condition, pure black and white, his tail nearly full length, and his upper bill had the large, light-colored growing patch of a male (pl. 1, fig. 2). He made squawks similar to those of my captive birds. Everything appeared well when I left.

The tragedy that overtook the family during the morning may be reconstructed from the chance observations of another bird watcher,

Mrs. Iris Darnton. At 10:30 a.m. Mrs. Darnton was attempting to photograph the parent hornbills where I had seen them earlier. The young one was perching on a low branch by a roadway. He flew with some difficulty to a higher perch. At this moment an intruding female hornbill attacked the young one and the two fell grappling to the ground. The parents made a great commotion. Their young one lay flat on the road, but soon flew onto the lawn, then into a low tree. After 5 p.m. I came to the gardens and found the family where last seen by Mrs. Darnton. The young bird was perched precariously near the top of a spindly tree and one foot hung limp and useless. He was using half-spread wings to maintain his perch. The male parent made a great noise when he saw me, but soon quieted down, hopped closer, and fed the young one four fruits. Ten minutes later he tried to feed him again, but without success. The mother bird did not attempt to feed the young one. She remained inactive. A foreign female hornbill stayed about 50 feet away. On the following morning I found the parents in the same area, but the young bird was not in the trees, so I searched the underbrush and found him on the ground. When placed on the lawn, he was unable to fly. The male parent swooped repeatedly at my head. I was reluctant to take away the young bird, but it was obvious that any passing dog or individual could kill it. I therefore took it home. Plate 1, figure 2, shows his appearance 2 days after leaving the nest. I estimated that he was 10 to 11 weeks of age, using as a guide my captive male of known age. One of his feet was broken. When placed in a splint, it healed completely in 3 weeks. This bird was the only one of my four captives that did not become tame.

Parental devotion.—No large hornbills had come to our garden regularly since departure of the roosting pair in October. However, from April 1 until May 15, when we left, a pair of hornbills came every day, often remaining for some time. I soon recognized the male. It was the one I had watched for 4 months in the Botanical Gardens, which were 2 miles away. The parent hornbills had located their young in his outdoor cage, and our garden resounded off and on all day with their wailing and commotion. They perched on adjacent trees, and frequently swooped down low over the wire. "Mutesa," as we called the young one, never responded in any perceptible way.

TERRITORY, AND RELATIONS OF HORNBILLS WITH ONE ANOTHER

Specific interference.—Nesting hornbills were interfered with by members of their own species to a surprising degree. Experiences at nest 5 illustrate the persistence of such interference. On November 6

the pair of hornbills were working on their nest late in the afternoon. An adult male kept coming into the tree and the male in possession repeatedly drove him away. By November 8 the female was walled in, and a more serious attempt at interference was now made by a foreign female. I first noticed her on November 19. She was following the male and lighted in the nest tree when he lighted above his nest hole. On November 23 the same course of events took place, except that the male was less tolerant. He fed his own mate, then drove the intruder away. A week later I again saw her fly in close behind the male and light 25 feet from the nest hole. The male gave his mate a piece of bark followed by some fruit, and then bounced from one branch to another toward the foreign female. The intruder called and the female within the nest screamed a number of times. I wondered whether the interloper could seduce the male, but from subsequent observations it seemed unlikely that she would. The male returned again to the nest hole, and a few minutes later was in the upper part of the tree knocking about on dead branches until he dislodged a piece of bark. He clamped his bill on the bark until it was largely fragmented. Then he moved toward the foreign female. If he presented the bark, one would suppose that she had some attraction for him. After a moment, however, he changed his direction, flew down to the big limb below, bent over the nest hole, and gave the token to his mate, accompanied by a feeding chuckle. Subsequently he returned to perch quietly within 8 feet of the intruding female. At 7:30 a.m. the two of them flew away together. As the nesting season progressed, he became less tolerant of her intrusions. On my next visit, a week later, he made several swoops in an effort to drive her away, but she was not discouraged. On February 3 I again watched her fly in behind the male and alight in the nest tree, making considerable noise. The male stopped feeding his mate, swooped at the interloper and drove her down toward the ground. However, when he flew away, she followed a short distance behind. It generally appeared that her interest was in him rather than in the nest. On March 2 I observed a more serious situation. Late in the afternoon I found a foreign female clinging to the nest entrance. This time she was alone. She worked industriously, removing debris from the entrance and knocking from the cement wall chunks which she broke in her bill before dropping them. There was no noise. After 5 minutes the male arrived and she flew a short distance away. He tossed some debris from the entrance, then drove the foreign female to another tree, flying at her so hard that he knocked leaves from intervening branches. He returned to his nest with a small stick held like a cigar.

His mate, who had remained silent, now began her wailing screeches. I also heard her bill tapping. The intruding female, persistent as usual, had followed the male back to the nest tree. In a few minutes he flew at her again, flying faster than hornbills usually do as he chased her from one tree to another. Five days later, mother and young emerged from the nest. As already related, a foreign female attacked the young bird and apparently broke its foot. After I had picked up the helpless young one on March 9, I returned to the Botanical Gardens late in the afternoon. The pair of hornbills were perched side by side in their nest tree. Not long after I heard a great flutter of wings. I looked back to see both members of the pair pursuing a foreign female. This was the last I saw of her. When the parents later came to our garden, she did not follow. I have presumed that the same foreign female was involved in all these incidents relating to nest 5. This presumption was based on her consistent behavior, general appearance, and bill shape. I never saw another female with which to compare her near the tree.

At 5 p.m. on January 26 I witnessed an intrusion by a pair of hornbills. A foreign female was on the lower rim of the nest entrance, poking her bill about the aperture. She made no noise. After some minutes a foreign male lighted on a limb above. He had a fruit in his bill tip. The female moved toward him, took the fruit, and kept offering it down inside the hole. It was not accepted. The foreign female would toss the fruit about in her bill, then try again. Finally the rightful male returned, drove the intruding pair away, and fed his mate a number of fruits. The whole incident appeared odd. I wondered whether the foreign pair were unsuccessful nesters, who, having a strong, though thwarted instinct to feed something, dropped in on the female in nest 5.

Interference by foreign hornbills was not limited to the nest in the Botanical Gardens. It happened not infrequently at other nests. A pair of hornbills were involved in each of the following intrusions. On November 19 a foreign pair were perched by nest 4 in Mpanga Forest. The female flew to the entrance, clinging to the lower rim with tail outspread for support. She then gave some hard pecks against the mud wall and grappled at bill point with the female inside the nest. Neither bird made any noise. However, when the intruder withdrew, the nest owner rattled her bill in the entrance. The foreign male sat quietly by without participating. In a period of 10 minutes the intruding female attacked the nest entrance 12 times, but did no significant damage. In the next 5 minutes she attacked only twice. Then the rightful male returned and drove the trespassers away.

Since this episode took place early in the nesting period, I conjectured that the foreign pair had, perhaps, not found a suitable nesting site and the female was trying to take possession of one already occupied. A second episode was difficult to interpret. It took place late in the nesting period, on January 23. I saw a foreign pair fly into the tree containing nest 15. The male repeatedly bent over the nest rim and there was a rattling of bills. He produced a "cherry" at his bill tip. Then he either gave it to the nesting female or dropped it into her nest. The female rattled her bill at the strange male. Ten minutes later the foreign female swung dramatically on a long tangle of epiphytic roots, then landed on the nest rim. This was the only time I ever saw a pair of foreign hornbills perched together on a nest. The intruding female wagged her bill vigorously in the opening. A few minutes later the owning male swooped in and drove the intruders away. He fed his mate some yellow fruit. She now screamed repeatedly.

On one occasion I saw a lone male attacking a nest. This was on November 21 at nest 6 in Mpanga Forest. The foreign male came quietly to a limb above the nest, then dropped to the nest rim. He appeared wary, bending his head to one side, then to the other, as he hung his head down to look through the entrance. The female had her bill ready but made no noise. He finally struck at the cement, then sparred with the female within the nest through the opening. I could hear their bills clashing. After 12 minutes the returning male owner drove the trespasser away. He had a leaf in his bill tip which he gave to his mate along with some fruit. It should be mentioned that a male may attack his own nest. At midmorning on November 28 the male from nest 7 flew down and rattled his bill in the opening. He was apparently in a bellicose mood for he next flew to a limb directly over my head, which was unusual. I could see his bill markings clearly. Meanwhile, his mate rattled her bill in the entrance.

Lone females were the most frequent intruders at hornbill nests. I often saw one at nest 11. She had a favorite perch 10 feet from the entrance where she would sit for some periods. The nesting female would rattle her bill and scream repeatedly, but her mate, on feeding visits, paid little attention to the intruder. On December 12 a foreign female perched calmly on the bole above nest 6. She repeatedly leaned down into the opening, giving the feeding chuckle eight times as she did so. The female in the nest rattled her bill. After 15 minutes the male returned and drove the foreign female away. A final and most unusual case of interference occurred at nest 16, which was 30 feet above the ground. On January 30 we had placed some

ladders and an African was preparing to climb up and open the nest. As we stood below, a foreign female flew in and lighted on the edge of the nest. I thought that the mother had already emerged, but it was later discovered that the mother and young were inside.

Territory.—Neighboring pairs of hornbills tolerated each other well. For example, nests 7 and 10 in Mpanga Forest were within 120 feet of each other and a third pair made persistent attempts to nest within an equal distance. Within this triangle I could watch activities of all three pairs at one time. They paid no attention to each other, their sense of territory apparently being limited to the nest tree and its immediate vicinity. Some trespassing was accidental and without interest in the nest itself. Thus nest 4 was centrally located in Mpanga Forest so hornbills engaged in their various activities frequently came near it. The male from this nest did more chasing than any other I had under observation. He had a peculiar habit of perching during the day within 10 feet of his nest hole. No other male perched close to its nest. Some might occasionally perch within 100 feet, but usually I saw males near their nest trees only on feeding visits. Females were frequently alone for 45 minutes to an hour at a time, and during these periods the nest tree was open to intruders. Hornbills may have a sense of territory in relation to roosting areas; I did not make sufficient observations to determine whether this was so.

Aggregations of hornbills.—Sometimes a number of hornbills would come together, usually owing to a common attraction such as a flight of insects, a fruiting tree, or a passing hawk. This did not appear to be true flocking. Nine was the largest number of hornbills I ever saw together. They were in our garden on August 26. Other observers told me that they had seen larger gatherings. On November 28 I watched two males and four females closely besetting a harrier hawk. A week later I came across what appeared to be the same group in the same area of Mpanga Forest. This time a band of redbellied monkeys were working along the forest edge. Six female and two male hornbills followed along with them sitting in the same trees but making no noise. I believe that the association was an idle one, for the hornbills were playing with sticks and showed no alarm. The excess of females was of interest. Pairs of hornbills were also frequent during the nesting season. I wondered if there had not been enough nesting sites to go around. On February 15 I saw a curious association of two adult male hornbills. They came to our garden and hunted together closely, going over cracks and crevices in a big tree. Two

weeks later I found the same pair a mile away and still closely associated.

RELATIONS WITH OTHER BIRDS

Hornbills became much disturbed when a hawk or eagle appeared in Mpanga Forest. A crowned hawk eagle perched on a tall tree at the edge of the headquarters clearing. Then he sailed into the forest and was lost from view. An hour later I heard a great noise and found the hawk eagle surrounded by casqued and the smaller pied hornbills (*Tockus fasciatus*). None came closer than 20 feet. On November 28 I was watching nest 8 when I heard a number of hornbills making short flights from one perch to another. This drew my attention to a harrier hawk in a dead tree. Two female hornbills were perched within a few feet of him, one on either side. Two males were in the same tree. When the hawk flew, all four hornbills followed him closely but made no noise. The bird that upset hornbills the most was a great sparrow hawk. On December 11 he flew up close to me in Mpanga Forest, calling "ker, kee, kee" in plaintive fashion. Three male hornbills accompanied him. None of them made any noise. Whenever the hawk circled and returned, the hornbills pursued closely and even swooped at him. On January 2 I again heard the cry of the great sparrow hawk. When he lighted above me, a male hornbill lighted within 6 feet of him, and when he flew, two hornbills followed within 20 feet. Hornbills are occasional predators themselves. Their presence, however, seldom caused any disturbance among smaller birds. I saw one hornbill momentarily beset by sunbirds and colies when he was robbing a nest of the latter. Broad-billed rollers (*Eurystomus afer*) would pursue hornbills passing by the lake shore. These aggressive birds attack everything from anhingas to starlings.

FOOD

Fruit.—Food brought by male hornbills to their nests consisted largely of fruits, ranging in size from a pea to an olive. Some fruits, such as figs and pawpaw, were brought in as amorphous pieces. The elliptical fruits of *Canarium schweinfurthii* were conspicuous and prevalence of their stones on the ground were a helpful clue to the location of nest trees. I was able to collect various seeds and fruit stones by cleaning the ground below nests. Following is a list of all fruits identified. Such indigestible matter passes through the digestive tract of the hornbills and is expelled with the feces. This was observed in both wild and captive birds. I have never seen hornbills go near

water and my captives do not seem to know what it is. Apparently they get enough water from fruit.

FRUITS IDENTIFIED FROM SEEDS, STONES, AND PIPS RECOVERED FROM
FECES BELOW HORNBILL NESTS

<i>Canarium schweinfurthii</i> Engl.	<i>Antiaris toxicaria</i> (Pers.) Lesch.
<i>Pycnanthus angolensis</i> (Welw.) Exell.	<i>Chlorophora excelsa</i> (Welw.) Benth.
<i>Pseudospondias microcarpa</i> (A. Rich.) Engl.	<i>Eugenia jambolana</i> Lam.
<i>Maesopsis eminii</i> Engl.	<i>Dracaena steudneri</i> Engl.
	<i>Ficus natalensis</i> Hochst.

Animal food.—Bannerman (1953), writing of *Bycanistes subcylindricus*, states that "this bird lives entirely upon fruit, as indeed do most of the large hornbills." During initial observations I had no reason to doubt this statement. By closer watching, however, I found that hornbills take a wide variety of animal prey. On December 6 a male went from one low perch to another among our garden trees, sometimes only 7 feet from the ground. Five minutes later I saw him fly up from the foot of a jacaranda with a 5-inch lizard squirming in his bill. He flew to a perch over a native shamba. Here he tossed the lizard about in his bill for some time, holding it by the tip of the tail, then chewed along until he reached the head. Finally the hornbill lost hold and the lizard fell. In a feat of acrobatics, the hornbill fell down after his prey, disappearing from sight in the vegetation. Fifteen minutes later the bird was back in our garden. A completely limp lizard hung from his bill as he flew over the hill in what I suspected was the direction of his nest. On January 31 another male hornbill was hunting in our garden. He hopped onto a perch, looked around slowly in all directions, then hopped to another perch and did the same. After some minutes he flew to a thick bushy tree, where he scrutinized the foliage carefully, then hopped directly to the end of a branch where a mouse bird had its nest. The hornbill picked up a small egg with his bill tip, sent it flying back into his gullet with a toss of his head, then did the same with a second egg. To finish off, he seized some nest material and dropped it. What followed was an example of the delicate control casqued hornbills have with their bills. The male coughed up one egg from his gullet and held it again in his bill tip. By this time his mate had arrived in a tree across the lawn. He flew over to her, still holding the egg, and settling beside her, presented her with the egg; then heaved and presented her with the other, both intact. She swallowed both. On February 15 I watched two male hornbills hunting in our garden. A double-toothed barbet (*Lybius bidentatus*) was excavating in a tree when the hornbills flew

directly to the hole. One male repeatedly drove his bill into the excavation. I was not sure whether the barbet was inside or not. For the next 15 minutes the hornbills quietly examined the hole, knocked off dead bark, and searched leaves and seed pods. Their hunting was not successful while in the garden. However, hornbills probably catch other birds on occasion. On January 29 a male in Mpanga Forest glided to his nest with a sparrow-sized bird, chewed beyond recognition, hanging from his bill. He saw me and quickly flew away. My captive hornbills have been maintained to a large extent on left-over laboratory mice which they swallow whole. They appear to thrive on animal protein.

Hornbills catch insects both large and small. I found the remains of some insects which they had fed upon by examining fecal matter below nest 5 in the Botanical Gardens. Dr. V. G. L. van Someren was able to identify the following:

REMAINS OF INSECTS RECOVERED FROM FECES BELOW HORNBILL NEST 5

Dicranorrhina micans (Drury)
Longicornis beetles of cerambycid group
Rhyparobia grandis (Sauss.)—large cockroach
Long-horn cricket
Tenebrionid beetle, *Metallonotus*
Slender-winged mantis

Some were not adequate for species identification. Large bark beetles were a frequent finding. Activities of a male hornbill observed on February 1 indicated how these might be captured. For a half hour in midmorning he worked on the dead portion of a large tree. He would strike slanting blows to loosen a piece of bark, then pry under it and appear to pick out something from underneath. The next step was to knock the loose bark to the ground. This hornbill showed acrobatic skill, often leaning way over on its long legs, with head and neck outstretched, in an effort to reach more bark. He removed at least 3 square feet before flying away. Praying-mantis nests were not infrequent in accumulations below nest 5. They had come through the digestive tract more or less intact, as indicated by adherent feces.

I would not have supposed that casqued hornbills could catch small insects on the wing. They are, however, quite resourceful in this respect. On April 18 three hornbills were perched on a casuarina tree late in the afternoon. They were gulping at a close swarm of insects that were whirling about in a small cloud near the treetop. These insects were black-winged termites. Some were still moving upward

from the ground. The hornbills made a clapping noise as they snapped at the passing termites and were at the game for over 10 minutes. On May 1 I witnessed a similar spectacle, again late in the afternoon. Compact swarms of small insects (not lake flies) were hovering at the tops of tall trees adjacent to the Institute Compound. Smaller birds were catching them, mostly by perching on a topmost spray. These birds included splendid starlings (*Lamprocolius splendidus*), bulbuls (*Pycnonotus tricolor*), Abyssinian gonoleks (*Lanarius erythrogaster*), and didric cuckoo (*Chrysococcyx caprius*). Two casqued hornbills were catching insects along with the smaller birds. For over 20 minutes they kept turning their heads to snap at the swarm around them.

Dr. W. H. R. Lumsden has contributed an observation which further indicates the agility of these large hornbills. On September 6, 1953, he was in the woods of the Botanical Gardens. Three or four hornbills were perched about 60 feet from the ground. They would swoop down across an open space, pick up something in midair, then rise to a perch in an opposite tree. They were after winged ants which were swarming on ground and vegetation below the clearing.

SOME ANATOMICAL FEATURES IN RELATION TO FUNCTION

Some peculiarities of hornbill anatomy came to have more significance with continued watching. The large eyes are unusually mobile for a bird. Casqued hornbills can look up and down to a moderate extent without cocking their heads as many birds do. This gives them, by human interpretation, a more intelligent expression. The upper and lower eyelids are continuous and in sleeping this fused eyelid is pulled over the eye from back to front. The combined eyelids are white in adult females. Considering that the eye is dark and surrounded by blackish feathers, I have wondered whether these white eyelids enable the male to see his mate better when looking into a dark nest cavity. The head is covered by fluffy feathers, $1\frac{1}{2}$ to 2 inches long. These are used in emotional expressions and when fully erect the head is like a small, round feather duster. From front view the topmost feathers, which may be the only ones erected, may resemble two horns. My young captive hornbills demonstrate how these feathers may be used. If I toss grapes to them, Mpanga may grab them all. Zika, the female, then feels left out. This is obvious by her expression. Her head feathers stand straight out in all directions as though to say "Where do I come in?" When alarmed or excited, her head feathers lie tightly back. If she next investigates some object,

like a crumpled piece of paper, they stand out partially again. In young birds the feathers just above the eyes and forming the horns are brown. By the age of 10 months these are almost entirely replaced by black feathers.

The bill tip can be used as delicately as a pair of forceps. In females, only the tips may be in apposition, leaving a slightly open space for several inches behind. This space is more exaggerated in older females and may suggest, to a mild degree, the bill of an open-bill stork (*Anastomus lamelligerus*). At first I thought the space was due to wear. However, my captive Zika had this space at an early age when wear was not apparent. The bill tip itself is very sensitive. It is, for example, continually used to investigate strange objects. If I give my captive hornbills a fruit they have not seen before, they will toss and squeeze it in their bill tips for some time before swallowing. The bill of the male is huge, and that of a young one is larger than a female's before he leaves the nest. This is shown in the photograph (pl. 5, fig. 2) of two young hornbills, male and female, at 7 to 8 weeks of age. Plate 6, figure 1, shows Mpanga's bill at 6 months of age and plate 2, figure 1, at 10 months. The white patch is apparently an area of growth. With some transillumination one can see that it is full of blood vessels. The patch becomes smaller in older males. No one knows, as far as I am aware, how long it takes the bill of the male to reach full development, with a forward projecting knob. At present I can only speculate on the function of this huge structure. It would appear to have no strictly practical use, for the smaller bill of the female serves more immediate functions. Her bill not only is used to plaster the wall of the nest, but is also a formidable weapon for defending the nest opening. Its inner capacity is no less than that of the male's. In addition, males and females are equally adept at catching small objects with their bills. I wonder, therefore, if the casqued bill is not chiefly sexual in function. Possibly it is comparable to the mustache stripe of the male flicker or the red breast of the cock robin. In this sense it would serve to release behavior patterns in the female which promote successful breeding and pair formation.

The feet of hornbills, with three front toes somewhat webbed, do not grasp tightly. I have never felt any real grip from the birds perching on my arm. Hornbills can, however, hang down from a perch, almost parrotlike, without losing their hold. The long tail is remarkable in that it can be neatly folded over the back. This adaptation is convenient for females walled within nest cavities, as is the fact that they are a third smaller than males.

DISCUSSION OF FACTORS CONTROLLING HORNBILL POPULATIONS

Birds such as hornbills which rear a single young one are, one may suppose, relatively safe from enemies. This was probably true before the original rain forests had been cut. A female walled in a nest 70 feet above the forest floor, in the trunk of a huge tree without lower branches, is in an almost impregnable position. Such trees, however, are now entirely absent over large areas. Natives' shambas, elephant grass, and patches of second growth cover the countryside, leaving only thin fringes of large trees along lake shore and swamp. Eastern Uganda is good agricultural country and the native population is rapidly expanding. Interference by man's activities is, I believe, the greatest factor limiting hornbill populations. Mpanga Research Forest remains as a needed refuge. Even here, observations suggested that suitable nesting sites were way below the demand. Some pairs of hornbills were nesting in unfavorable situations. For example, nests 10 and 16 (table 1) were only about 30 feet from the ground and were easy to reach. Also, I continually saw pairs of hornbills that were not nesting during the nesting period. Two pairs tried without success to build nests in unsuitable locations. When nest 4 suddenly became vacant owing to the death of the male, another pair of hornbills took it over immediately. Some of the incidents of specific interference already narrated indicate the degree of competition. The disastrous effects of forest destruction on casqued hornbills is well described by Capt. C. R. S. Pitman (1955, personal communication). He writes that "ever since I first went to Entebbe in 1925 forest destruction in the vicinity of Entebbe and Kisubi, and in fact all along the NTB-Kampala Road, has been on such an appalling scale, that annually large numbers of trees, with the best nesting sites, are being destroyed. *Bycanistes* therefore is constantly having to move farther and farther afield to find suitable nesting sites. When I first went to Entebbe there must have been at least two dozen *Bycanistes* nests within a 2-mile radius . . . but now good nest sites are fewer and far between and *Bycanistes* resorts to hollows, some readily accessible, which it would have ignored in the past."

Fortunately Africans in eastern Uganda do not molest birds to any extent. Ease of growing food and comparative prosperity probably puts less pressure on them to do so. But in Bwamba, where hornbills were considered fair prey, I continually came across Pygmies and other natives wandering about with slingshots and small bows and arrows. Under these conditions I found the birds more wary and difficult to observe than near Entebbe.

COMPARATIVE STUDIES OF OTHER HORNBILLS

Genus Tockus.—There were two other species of hornbills in the vicinity of Entebbe, the crowned hornbill (*Tockus alboterminatus*) and the pied hornbill (*Tockus fasciatus*). These two smaller hornbills are somewhat similar in size and appearance. I could never discover any basic difference in their habits. Their high piping cries, erratic type of flight with many rises and dips, and greater concentration on insect food readily distinguished them from casqued hornbills. All three species occurred in the same stretches of open country and forest.

On March 20, 1955, I noticed a crowned hornbill flying through Zika Forest. He lighted on a treetop, then suddenly dropped downward. Searching the area, I found a leaning tree with a bole, 40 feet above the ground, with a 2-inch hole in the center. There was almost no suggestion of a mud wall. I watched for 20 minutes. At one time white feathers closed the entrance as the female pushed her vent to the opening, and a stream of excreta shot out. The maneuver was the same as I had witnessed with *Bycanistes*. Later the male returned to perch on the bole and feed his mate a large insect (mantis?). He did not linger, the briefness of his visits apparently being due to the fact that he carried only one item in his bill tip; there was no heaving up of fruits from the gullet such as characterized visits of male casqued hornbills to their nests. On March 25 an African, well trained at the Institute, climbed up and inspected the nest for me. There were three white eggs. The mother bird, when poked, backed to the rear of the cavity. Unfortunately, preparations for leaving Africa prevented an adequate study of these birds. I am indebted to Dr. Friedmann (1925) for the following account, hitherto unpublished, of the opening of a nest of this species in Kenya Colony.

On April 7, at Taveta, some natives cut down a large tree in which there was a nest of this hornbill containing the adult female and two young birds. The nest was about 50 feet up in the tree and was in a large hole, the entrance of which measured roughly 10 inches in long diameter and 3 inches wide. This entrance was plastered up with dry mud, bird feces, and bits of bark all mixed together, leaving an opening about 2 inches long and 1 inch wide. As I picked away at the mud the adult female pecked at me with its bill, about an inch and a half of which could protrude through the opening. When finally I opened the nest and took out the birds I found that the two young birds were of different ages, the older of the two [pl. 6, fig. 2] being feathered on the back, wings, sides, legs, and crown, while the tail feathers were free of their sheaths for their distal thirds and the sheaths of the neck and breast feathers were beginning to burst. The other bird was less well feathered, the wings and flanks being the only parts really well covered. The tail feathers were about the same as in the older bird and the under

tail coverts in both were well developed. In both nestlings the bill showed no trace of a casque and was a yellowish-horn color; the feet were dark lead color; the skin light pinkish; the iris bluish gray. The tail folded up against the back so well as to look like a definite adaptation to living in crowded quarters. In fact it seemed to be muscularly easier for the birds to hold their tails up than to straighten them out [pl. 6, fig. 2]. One of the nestlings when put on the ground fell over forward on its head and breast and the tail remained sticking straight up in the air as though the bird were unable to drop it into what would be considered the normal position. The adult female when about to enter a nest before egg-laying usually begins to molt and is for some time thereafter in quite a helpless condition. New feathers grow in while the eggs are incubating and the young growing to the flying stage. The female taken from the nest had all the new tail feathers well developed but all of them were still basally enclosed in their sheaths. The bird was still missing the outermost secondaries and innermost primaries but the other remiges were there, most of them more or less still in their sheaths basally. The bird could fly only very poorly and seemed dazzled by the light. Several times I let it go and each time it flew or rather half fluttered, half flopped through the air very laboriously for a short distance and stopped by smashing against a tree or the side of my tent.

I had some evidence that pied hornbills also breed in March. From November on I had been observing a pair of casqued hornbills in the Botanical Gardens and had kept watch on a squirrel hole 50 feet up in a nearby tree. It was not until March 1 that I noticed a pair of pied hornbills showing any interest. At 7:30 a.m. a pair were preening nearby. Between them they made 10 visits to the hole, poking their bills inside. When a crowned hornbill appeared, they chased it away. The following day the pair were at the hole morning and evening. On March 8 I saw them putting their bills into the hole and tossing out debris. I had no subsequent evidence that the pair nested. The hole may have been occupied by a squirrel which I had seen using it previously. Apparently smaller hornbills may compete with hole-nesting mammals. On February 18 I was driving near Kaboona, in the arid country of Karamoja, when I noticed a pair of Jackson's hornbills (*Tockus jacksoni*) catching insects and flying to a 2-inch hole in a dead tree. When I returned 4 days later the pair were still inspecting the nest hole. Thinking young hornbills might be in the tree, I cut it down. To my surprise, the cavity contained a mother bush baby (*Galago senegalensis*) with a mouse-sized young one. These limited observations may have interest because I could find no breeding dates for these three species of *Tockus* in eastern Uganda.

The investigations of Gordon Ranger (1949-52) offer an opportunity to compare the habits of *Bycanistes* with those of *Tockus* in some detail. These investigations on African hornbills are the most complete known to me. They have extended over many years and concern

another crowned hornbill (*Tockus alboterminatus*) which occurs in South Africa. Comparisons will be made first in regard to differences of behavior, then to points of similarity with *Bycanistes*. All observations and quotations on the crowned hornbill are from Ranger's publications.

Differences in behavior between Bycanistes and Tockus.—(a) Crowned hornbills have a definite territory which is fairly extensive, is defended against trespassing hornbills, and is maintained year after year by the same pair which temporarily share it with the offspring of each season. I found little evidence that *Bycanistes subcylindricus* maintains a definite territory other than the immediate vicinity of the nest tree.

(b) Crowned hornbills live more extensively on insects. This greater consumption of animal protein is reflected in their white excreta. In feeding his mate at the nest, the male carries the food, usually a single insect, at his bill tip. He does not load his gullet, then cough up fruits one at a time as do male casqued hornbills. Furthermore, crowned hornbills make casts of indigestible seeds, pips, and hard parts of insects. Casqued hornbills, on the other hand, pass everything out in the feces—even large fruit stones, whole baby mice, and mantis nests.

(c) There are a number of differences in the manner of plastering nest walls. Crowned hornbills make plaster of feces, finer soil from the floor of the nest, and insect remains. According to Ranger "the female does not swallow anything for the purpose of disgorging it in the form of plaster," and "the male plays no part whatever in plastering the nest hole." *Bycanistes* collect soil and lumps of earth from the ground. Both sexes do this, but the male brings the most and is a kind of "bricklayer's helper," supplying his mate who does the actual plastering.

(d) A distinction between *Bycanistes* and *Tockus* lies in the time of emergence of the female from the nest. Ranger (1955, personal communication) has extensive data on this subject. He has found that the female may emerge 62 to 74 days after being walled in. At this time the precocious young reseal the entrance. Both parents then feed the young which emerge 19 to 34 days later. Moreau (1936) has collected similar information in regard to *Tockus deckeni* and *T. alboterminatus*.

Similarities in behavior between Bycanistes and Tockus.—A close relationship between the two genera of hornbills is indicated by similarities in their behavior patterns. Many of Ranger's descriptions (1949-52) of the habits of *Tockus alboterminatus australis* apply

equally well to *Bycanistes subcylindricus*. I have quoted a number of these verbatim.

(a) Food. The crowned hornbill's handling of larger prey is the same as for *Bycanistes*. Speaking of a grasshopper, Ranger writes "the hornbill . . . subjects the creature to prolonged chewing and pulping between the mandibles before swallowing, turning it about and tossing it to secure new holds. . . ." Chameleons and nestling birds are treated in the same manner. Among insects taken by crowned hornbills, those as diverse as winged termites, long-horned beetles (cerambycids) and, curiously enough, mantid egg cases were all fed on by *Bycanistes*. After feeding, cleaning "is performed by scraping and wiping the outside of the bill against a branch."

(b) Roosts. The crowned hornbill has roosting sites which are used in rotation. Each member of the family, however, has its own private perch. The two casqued hornbills in our garden always used the same individual perch each night. Like *Bycanistes*, the crowned hornbill is not an early riser. The birds stretch and make gruff utterances to each other for some time in the morning before leaving their roosts.

(c) Play and agility. The following odd traits are also true of casqued hornbills. Ranger wrote that the crowned hornbill reveals "its dexterity when by diving it recovers an object that falls from its bill before it reaches the ground." Speaking of a captive bird he writes that "Conkie was adept at catching objects cast at her over intervals of many yards." The bill whacking of male casqued hornbills was a characteristic sound in the forest. Ranger wrote as follows of the crowned hornbill: "The meaning of the exaggerated scraping of the bill against a branch, indulged in more particularly by the male, has not become apparent."

(d) Basking. "The foliage bath is followed by basking, advantage being taken of the sun's appearance in a clouded sky, but basking is independent in purpose. The body with wings extended is relaxed and spread limply upon branch or foliage, the head and neck upturned. Conkie assumed the most limp, lifeless, unbirdlike attitudes, neck curled with throat uppermost, eyes obscured by the relaxed third eyelid." Such postures are the ones assumed by my pet hornbill, Zika. It is not a matter of drying her plumage but love of sunshine for its own sake. As soon as the sun comes from behind a cloud, whether she is indoors by a window or outside, Zika assumes the grotesque attitudes so well described by Ranger.

(e) Courtship. In describing breeding habits of *Bycanistes*, I have included various activities under a heading of courtship and main-

tenance of the pair bond. This is a matter of interpretation. Ranger uses other phraseology, but the activities he describes are similar. For example, he wrote of the following behavior as having taken place 26 days before final entry. "Investigation of a knocking and rattling near Site I disclosed the hornbill pair, one striking its bill with vibratory rapidity against a branch. The side of the terminal part of the bill was used, and the point, vibrating, traveled around the surface of the branch till in turn the opposite side came into play . . . then the other bird . . . became enlivened and extending its bill performed the same rattling action." Ranger believed this rattling was the same motion employed in plastering and made special note that both sexes were involved. I am not sure whether this performance is entirely related to the onset of nesting in *Bycanistes*. My captives, Mpanga and Zika, do a good deal of tapping. They began when 9 to 10 months of age and sometimes do it against my clothes. Ranger has stated further that his crowned hornbills made increasing visits to the nest tree as the season progressed. Such flights were initiated by the male. A new behavior was noted 19 days before final entry into the nest when the male began to present food to the female. This was done anywhere, not necessarily near the nest tree. Finally, bark presentation was frequent among crowned hornbills. Ranger found that the female would take bark with ready interest from her mate, then bite it to pieces.

(f) Intruders. I have described intrusions on nesting casqued hornbills by members of their own species. Apparently a similar phenomenon takes place among crowned hornbills. Speaking of a feeding visit Ranger wrote "the male and a young intruder arrived, and this drew a single sharp cry from the female. . . . The male then delivered an item and resumed his chasing of the intruder." This male subsequently delivered "13 items of food and bark, but all the time was worried by the young trespasser who followed him again and again to the nest. . . ." I was unable to tell whether the female intruders I saw by *Bycanistes* nests were young birds or not. The male intruders were all adults. Ranger has also written of the nesting female rattling her bill in the entrance. He describes this "habit rattling" as useless activity. This was not true of casqued hornbills. Every time I saw a female rattling her bill there was some cause, such as presence of intruders, to evoke this alarm signal.

(g) Plastering. Photographs of nest entrances presented by Ranger show that the cement walls look much the same as those constructed by *Bycanistes*. The female crowned hornbill has the same technique of plastering. "Always the bill works rapidly in vibratory

fashion, the side of the end portion . . . beating against the surface, to which the moist dung is applied." Ranger has also noted that the cement walls are built up in layers.

Ranger has been fortunate in having many years in which to study crowned hornbills. If I had had at least a second year to study *Bycanistes* I should have been specially interested in finding out (1) whether these hornbills remain paired from one season to another; and (2) whether the same pair returns to the same nest tree in succeeding years. Both of these situations, true for the *Tockus albotermis*, presumably hold for casqued hornbills.

Ground hornbills.—I had only casual views of the huge ground hornbills in Karamoja and in Murchison Falls National Park. These form the third main group of hornbills that occur in British East Africa. The following unpublished account of *Bucorvus cafer* (Schlegel) is contributed by Dr. Friedmann. It is of interest from the point of view of comparative biology.

This giant hornbill was seen in rather small numbers in the open bushveldt at Taveta, Kenya Colony, during March and April. The birds were usually seen walking around on the ground in loose groups of three to six individuals. They really walk, not hop. In East Africa they are protected as scavengers and are not molested by big-game hunters and settlers. Although they feed on the ground they sleep high up in tall trees and can fly remarkably well for their bulk. The original "take-off" seems to give them some little difficulty, but when once under way they fly more directly than do most hornbills, their heavy wings causing a very audible *woof woof* with every stroke. The call note is a deep *boom boom*, a rather hollow, and reverberating note. During the mating season the birds become more vociferous and call to each other with great frequency.

The natives in Kenya Colony have a story to the effect that the female ground hornbill says, "*boom boom, I'm going home; boom, I'm going home*" and the male counters with, "*you always say that; boom, you always say that; I'm tired of hearing it; go on home; boom boom.*" It was, therefore, with considerable interest that I learned from Mr. Rudyerd Boulton that the natives in Angola have another interpretation of the calling of these birds. They say that the female says, "*boom boom, I'm going home, I'm going home,*" while the male replies with, "*you must not do that, you must hold up the corn.*"

Like all hornbills these birds feed by picking up bits of food with the bill, then tossing it in the air and catching it far down in the bill or even in the open mouth as it descends.

DISCUSSION OF HORNBILL BIOLOGY

An early impression at Entebbe was that many of the nonmigratory tropical birds, from hadadas (*Hagedashia hagedash*) to red-bellied shrikes (*Laniarius erythrogaster*), remained paired throughout the year. Casqued hornbills were usually encountered in pairs. They are presumably mated for life and one would like to know when pair

formation takes place. It may have no immediate relation to the breeding season. I had three young captives, hand-reared and approximately of the same age, in a cage at Entebbe. Mpanga and Zika were definitely paired before they were 3 months of age. Zika would work through Mpanga's throat feathers as he let his head fall back, then he would do the same for her. The other hornbill, and later a fourth, both males, led independent lives except for roosting. Unnatural conditions undoubtedly favored this early pairing. Young birds, however, do not necessarily pair up when confined together. This was shown by three magpies (*Pica pica hudsonia*), taken before they left the nest, which I kept in a large cage in the same manner as the hornbills. They showed no inclination to pair.

Maintenance of close pair formation demands mutual attentions. When casqued hornbills are perching in different trees, the members of a pair are almost always in communication with each other, sometimes only with single notes such as "cak" or "ugh." When together, mutual preening, in which the female may take the lead, is a common activity. This preening about the head and nibbling of feathers under the throat went on regardless of the time of year. I saw it going on at dusk in the pair which roosted in our garden in October and again with the pair in the Botanical Gardens, on the day the female emerged with her young one in March. It took place early in the life of Mpanga and Zika.

I have interpreted as courtship, activities which bring a pair of hornbills into the rhythm needed for the close cooperation involved in nesting. The lead is taken by the male. He feeds his mate and presents her with sticks and pieces of bark. In addition he becomes noisier in his calls and wailing. Similar activities are not uncommon to the courtship of many groups of birds. The male hornbill also takes the lead in exploring possible nest holes. By his cries and wailings, and his flights back and forth, he tries to induce his mate to look at them.

Stonor (1937) has given an interesting account of a pair of trumpeter hornbills (*Bycanistes buccinator*) which attempted to breed in the London Zoological Gardens. Courtship consisted principally of the male feeding the female. She would fly down to the feeding dish, then wait expectantly for him to feed her. Sometimes he would do so. At other times he would swallow the food himself. Then, as if stricken with remorse, when she would fly to a higher perch, he would at once follow to feed her a morsel. Stonor wrote of a "curious ceremony, wherein the female flew up from the ground with food in her beak which she passed to the male, who then returned it to her,

when she swallowed it." I have previously described an almost identical situation which took place in Mpanga Forest.

Important differences in appearance of hornbills are located about the head, the region which can be seen best through a nest opening. Head feathers in birds of all ages express emotions. In young birds the feathers at the base of the upper mandible are brown instead of black. The huge, forward-projecting casque of the male is his chief sexual characteristic and white skin around the eye is a peculiarity of the female. Many African hornbills have brightly colored patches of skin and wattles about the head and neck. These, however, are entirely lacking in *Bycanistes subcylindricus*. One would like to know what part these bright colors may play in courtship performances.

Cotition in one pair of casqued hornbills took place without any special courtship other than some touching of bills. The pair were returning to their nest, after gathering termite earth. Moreau (1936) found that copulation took place in *Bycanistes brevis* just after the female had emerged from her morning's work and about 10 days before the nest wall was complete.

Good nesting sites are probably used annually. Pitman (personal communication, 1955) believed that the nest hole that I watched in the Botanical Gardens had been used in 1947 and in 1949. At nest 1 the pair tried for weeks to close the opening. Interest, however, began to fall off a week after cotition, a situation that paralleled one described by Moreau (1936) in Usambara. Pairs of *Bycanistes brevis* tried for 2 years to nest at one site without success. "In both years," Moreau wrote, "building continued after copulation had taken place, and when work had ceased, both birds still showed a keen interest in the nest hole." Failure at the nest in Mpanga Forest may have been due to the large size of the opening. Other factors could have been operative also. The pair, or perhaps only the female, for example, may have been young and inexperienced. It is difficult to follow Moreau's hypothesis that in Usambara, failure to complete nests was due to the male's running out of saliva.

Casqued hornbills probably lay two eggs to insure that a single healthy chick is produced. The young bird becomes so large that the nest might be overcrowded if two chicks survived. Crowned hornbills have two to three young. The mother, however, leaves the nest some weeks ahead of time. This not only makes more room for the young but enables her to help in the feeding.

The length of time a female is walled in a nest (119 days for nest 5) does not appear unusual for a bird of hornbill size to lay eggs, incubate, and rear a young one. One can use Wahlberg's eagle

(*Aquila wahlbergi*) for comparison. It is approximately the size of a casqued hornbill and has been studied by Leslie H. Brown (1952) in Kenya Colony. He observed an incubation period of 46 days and a fledgling period of 72 days at a nest where a single eaglet was raised. This gave a total of 118 days. The total time is about the same as for the casqued hornbill, which, I have estimated, leaves the nest when 10 to 11 weeks of age. I would have supposed that young hornbills would grow more slowly on a fruit diet—they had animal food only occasionally. However, as indicated by white matter in the feces, they may have had more animal protein, particularly in the form of smaller insects, than I realized. It was almost impossible to feed my young captive hornbills on fruit alone. The volume required was exhausting. We reduced the number of feedings, first by coating pieces of pawpaw with powdered milk, then by giving each bird six to eight half-grown mice a day.

Intrusions of foreign hornbills on nesting pairs of their own species presented an interesting study. In a few instances the intruders came in pairs. There were many free pairs of hornbills throughout the nesting season and I wondered if these were not an index of an increasing shortage of suitable nest trees. Intrusions by single female hornbills were more difficult to explain. At one nest the same female apparently stayed around for months, and possibly attacked and crippled the young one soon after it left the nest. Several explanations suggest themselves. First, intruding females may have been offspring of the season before, unwilling to leave their parents or, second, they may have been unmated adults attracted by a seemingly lone male; possibly they fell into both categories. Some of them seemed to be more attracted to the nest itself and others to the male, coming and going with him as he made his feeding visits. I had an impression that there was an excess of females in the hornbill population.

In conclusion, the pleasure of watching hornbills comes from their love of play, unexpected agility, clownishness, and seeming intelligence. This last quality is difficult to assess. The intelligence of the crow family is well recognized. I have kept tame blue jays, crows, and magpies and rate my captive hornbills on the same level. Both groups are playful and curious, examining new objects with interest. They have a wide range of vocal expression. The large eyes of hornbills, together with expressive movements of head feathers, give an impression of intelligence which is hard to disregard. Whatever their mental capacity, however, it is difficult to see how these birds can adapt themselves to civilization, as they are destined to inhabit large

forest trees. My unusual opportunity to study their breeding and other habits in the vicinity of Entebbe has been most fortunate.

SUMMARY

Sixteen nesting pairs of casqued hornbills (*Bycanistes subcylindricus*) have been studied in the vicinity of Entebbe, Uganda. An unusual concentration of nests was found in the Mpanga Research Forest.

In courtship the male presented his mate with food and bits of bark or sticks. Mutual preening and calls back and forth were important in maintenance of the pair bond.

The male did the pioneering in exploration of possible nest sites and tried to entice the female to them with wailing cries. Plastering was done by the female from the inside of the nest cavity, using a rapid tapping with the side of her bill tip. Both sexes flew to the ground to collect dirt for building. Most of this, however, was done by the male. He attended the female, furnishing her with pellets for construction of the nest wall. Termite earth was preferred for building.

Two eggs are laid. Although both may hatch, only one chick is raised.

Male hornbills feed their mates about every 30 to 60 minutes, heaving up fruits held in their gullets. Often a stick or piece of bark is presented first.

Nest sanitation is accomplished by female and chick expelling feces through the entrance. The female may also toss debris out with her bill. If such debris collects outside of the entrance, it is regularly cleared away by the male.

Ants which swarm in some hornbill nests may act as scavengers and keep down insect fauna.

Females walled within nests can be extremely noisy if alarmed.

Observations made at one-third and two-thirds through the nesting period indicate that females have a gradual molt. Two females removed when two-thirds through their nesting could fly readily.

The total period a female was walled in one nest was 119 ± 2 days. A young hornbill, captured two days after emerging, was in full plumage.

The majority of casqued hornbills in eastern Uganda probably begin nesting in September and break out in January.

A hornbill territory is confined largely to the vicinity of the nest tree.

Occasionally a foreign pair of *Bycanistes* would visit a nesting female and attempt to feed her.

Lone female hornbills interfered persistently with a number of nesting pairs. At one nest this interference had serious consequences.

Male hornbills fed their mates largely on fruit but also caught insect and vertebrate prey. Lists are given of such fruits and insect remains as could be identified.

Roosting habits are described for one pair before and for a lone male during the nesting season.

Casqued hornbills were much alarmed by hawks and eagles.

They prefer the largest of forest trees to nest in. Rapid destruction of forests in Uganda threatens the future of these birds.

Three hornbills, removed from nests when 6 to 7 weeks of age, have been reared in captivity, largely on a diet of animal protein. The exact age of one captive was known. Two of them have remained closely paired from the age of 3 months. Bill tapping and plastering against the walls of their cage were done by the male and the female, beginning at 9 to 10 months of age.

A comparison has been made of *Bycanistes* and *Tockus*. There are many points of similarity in the habits of the two genera.

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CRUSTACEAN METAMORPHOSES

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U.S. Department of Agriculture



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CRUSTACEAN METAMORPHOSES

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INTRODUCTION

The review of crustacean metamorphoses given in this paper contains little that will be new to carcinologists, except perhaps a few accompanying unorthodox ideas. The paper is written for students in general zoology and is recommended reading for entomologists, who commonly think of metamorphosis as a phenomenon pertaining particularly to insects. It is true that the metamorphoses of insects and of crustaceans have no relation to each other, and have little in common, but a preliminary discussion of both will help in arriving at a general understanding of the nature of metamorphosis as it occurs in the arthropods.

The first treatise on metamorphosis was written by Ovid in about the year A.D. 7, but the metamorphoses that Ovid described were mostly the transformations of members of the human species into animals, trees, or rocks, willed by the ancient gods or goddesses in revenge against some mortal that had offended them. The metamorphoses imposed on animals by nature are not punishments, extreme as they may be in some cases, but are beneficent changes of form to better accommodate the individuals of a species temporarily to a more advantageous way of living. The young butterfly, for example, transformed in the egg into a wormlike caterpillar, is not an elegant creature as are its parents, but from a practical standpoint the caterpillar is perfectly adapted to its chief function, which is that of feeding.

The metamorphoses of Crustacea differ essentially from those of insects in that they pertain to a much earlier stage of development. The young insect hatches from the egg usually with the definitive number of body segments. The insects are thus *epimorphic*; but if the young insect has taken on a metamorphosed form in its embryonic development, it appears on hatching as a creature quite different from its parents. Yet a caterpillar, for example, is actually a winged juvenile stage of the butterfly corresponding with the so-called nymphal stage

of a grasshopper. The principal difference between the two is that the wings of the young grasshopper develop externally, and those of the caterpillar grow internally within pockets of the skin beneath the cuticle. Likewise, a "legless" fly maggot has legs developing in pouches of the skin covered by the cuticle. A young grasshopper goes over directly into a mature grasshopper; the caterpillar, the maggot, and others of their kind, when full grown with plenty of food stored in their bodies, must undergo a second transformation in a pupal stage to be restored to the parental form. This is the usual course of metamorphosis among the insects.

Most of the Crustacea, on the other hand, hatch at an early stage of embryonic development, though at varying periods of immaturity, when they have only a few body segments and corresponding appendages. During their development after hatching they successively add new segments and appendages until the definitive number is attained. The majority of crustaceans are thus *anamorphic* in their manner of postembryonic growth, though a few are epimorphic.

Anamorphosis involves a change of form during development, but it is merely a way of growing, common to crustaceans, diplopods, and some chilopods. It should not be confused with changes of form that have nothing to do with progressive development toward the adult; such changes constitute a true *metamorphosis*. The metamorphoses of Crustacea are changes of form that the growing animal may take on at successive stages of its anamorphic growth, including the sexually mature stage of many parasitic species. In such cases, metamorphosis has been superposed on anamorphosis. As Gurney (1942) has said, "it may be assumed that development in the Crustacea was primitively a continuous process of growth and addition of somites and limbs, as we find it to be in some branchiopods, and that abrupt changes between successive moults leading to the origin of definable phases are secondary responses to changes in the habit of life of the larva and adult." Gurney notes an apparent exception to this rule in the Euphausiacea and some Penaeidae, in which the larva and the adult lead much the same kind of life. The successive phases of development in these two groups, however, are mainly stages of anamorphic growth; their only metamorphosis is the adaptation of the larval appendages for swimming.

Insect larvae may undergo metamorphic changes of form during their growth, but with the insects this larval *heteromorphosis*, commonly called "hypermetamorphosis," affects the fully segmented young insect, and is therefore not comparable to the heteromorphic larval growth of most Crustacea. Some metamorphosed young insects trans-

form directly into the adult, but most of them first undergo a reconstruction in a special, proimaginal pupal stage. Among the Crustacea there is no transformation stage strictly comparable to the insect pupa.

True metamorphic forms are not recapitulations of phylogenetic stages in the evolution of a species. An insect larva, though often wormlike in appearance, does not represent a worm stage in the ancestry of insects. A caterpillar has a modern insect head and mouth parts, a well-developed tracheal system, and wings growing beneath its cuticle. No worm, ancestral or otherwise, was ever thus equipped. Among the Crustacea also most juvenile forms assumed during the larval growth are temporary adaptations to a changed mode of life and are not phylogenetic recapitulations. Yet, it is true that former ancestral characters discarded somewhere along the line of evolution may appear in the ontogeny of the individual, and it is often difficult to determine what phases of development are recapitulatory and what are metamorphic aberrations. The following hypothetical example will make clear the distinction between the two, and will lead to a practical definition of metamorphosis.

If the eggs of birds regularly hatched into reptilelike creatures, which later transformed into feathered fowls, the change of form would literally be a metamorphosis; but, since birds have been derived from reptilian ancestors, it might be specifically a case of phylogenetic recapitulation. On the other hand, if there issued from the bird's egg a creature having no relation to anything in the avian line of adult evolution, but which still finally transformed into a bird, the change of form would be one of quite a different nature, and it is this kind of change that will be regarded as metamorphic in the following discussions. As here defined, therefore, *metamorphosis* is a structural change at any time in the life history of an animal that may be regarded as an aberration from the ancestral direct line of adult development which followed approximately the phylogenetic course of evolution of the species. In this case metamorphosis may affect the embryo, the larva, or the adult. Simple development without metamorphic interpolations might then be termed *orthomorphosis*.

In the higher Crustacea there is a tendency for hatching to take place at later and later stages of ontogeny, leaving a correspondingly lesser amount of development to be accomplished after the larva leaves the egg. Finally a condition is reached when body segmentation and appendage formation are complete or almost so at hatching; the animal then becomes epimorphic in its development. In an epimorphic arthropod, the embryonic development may proceed by the method of anamorphosis, or the entire body may be first laid down as a germ band.

In the second case segmentation appears later, usually progressing from before backward, suggesting that it represents a former anamorphic mode of segment formation in which the anterior segments are the oldest. Since anamorphic growth, either in the larva or the embryo, is characteristic of the annelid worms and recurs in so many of the arthropods, it was probably the primitive method of growth in the annulate animals.

The most immature larval form among the arthropods is the crustacean nauplius. For practicable purposes early hatching must be given up by terrestrial animals, unless they go back to the water to lay their eggs, as do the land crabs, frogs, and toads. The anamorphic myriapods do not quit the egg until they have acquired the adult type of structure and are equipped with a sufficient number of legs for terrestrial locomotion. The completely epimorphic spiders and insects are best fitted to cope at once on hatching with the conditions of their environment, and they have become the most successful of the land arthropods. Though some insects lay their eggs in the water and the young are aquatic, they are simply terrestrial forms that have become secondarily adapted in the larval stage for life in the water; they hatch at the same stage as their relatives on land.

The Crustacea are primarily aquatic animals; only a few have become adapted to a permanent life on land. The eggs of most species are laid in the water, and the newly hatched young must be capable of swimming; the adults can later adopt a bottom habitat if they acquire ambulatory legs. Considering the uniformity of the water environment of a swimming larva, there is relatively little inducement for a young aquatic animal to undergo adaptive metamorphoses. The metamorphoses of most crustacean larvae, therefore, are relatively simple as compared with those of insect larvae, which have a great diversity of habitats open to them. Parasitic crustaceans, however, are a conspicuous exception to this generalization.

As a rule small animals in the water are eaten by larger animals, but the small creatures have one recourse against their possible predators and that is to become parasitic on them. Parasites, however, have to be structurally adapted to a parasitic life, and consequently most parasites undergo metamorphic changes. Many of the smaller crustaceans have adopted parasitism, and the most extreme degrees of crustacean metamorphosis are found among such species, especially if the adults themselves remain parasites. Such adults in some cases have lost all resemblance to the ancestral forms of their race, even every mark of their crustacean ancestry. Moralists may cite the "degeneration" of such parasites as a warning of what parasitism may

lead to, but actually parasites are highly specialized for the life they lead by a simplification of structure and the elimination of all unnecessary organs, which were indispensable to their free-living ancestors. In fact, no sympathy need be wasted on "degenerate" parasites; give them credit for having found a simple and easy way of living, though at the expense of another creature. They have discarded all useless equipment, and some of them have devised most ingenious ways of attacking the host.

The control of metamorphosis by hormones has been extensively studied in insects, but apparently no comparable studies have been made on the role of hormones in the metamorphosis of crustaceans. It is well known that hormones are produced in the eyestalks of decapods, and the source of the eyestalk hormones has usually been referred to two organs known as the *sinus gland* and the *X organ*. However, from recent investigations (see Bliss and Welsh, 1952; Passano, 1953) it is now known that the so-called sinus "gland" is not a gland but a complex of the enlarged ends of nerve fibers proceeding from the X organ and from numerous neurosecretory cells in the brain, in the ganglia of the optic lobe, and in the thoracic ganglia. The sinus "gland" is therefore a receiving and distributing center for various hormones. Functions that have been attributed to these hormones include the movement of pigment in the compound eye, regulation of chromatophore activity in the integument, control of moulting, and the rate of development of the ovaries. Knowles (1953) gives evidence that the chromatophores are activated also by neurosecretory cells in the region of the tritocerebral commissure and the postcommissural nerves. The control of moulting by lengthening the period between moults was attributed by Passano to the X organ, which is itself a neurosecretory tissue in the proximal ventral part of the medulla terminalis of the optic lobe. Removal of both sinus "glands" has no effect on moulting since the hormone can escape from the cut ends of the nerves. Panouse (1946) also, in a study of *Leander*, had claimed that the "sinus gland" produces a hormone that normally blocks the growth of tissues and thus causes a lengthening of the intermoult period and retards the maturing of the ovaries.

From later work by Gabe (1953) and Echalié (1954), however, it now appears that moulting, at least in the Malacostraca, is controlled by a pair of ductless glands in the antenno-maxillary region. These glands, discovered by Gabe, are named by him the Y organs, and were demonstrated to be present in 58 malacostracan species, ranging from *Nebalia* to the decapods and stomatopods. In species in which the excretory gland is maxillary, the Y organs are in the antennal seg-

ment; in those having antennal glands they lie in the second maxillary segment. Each gland is implanted on the epidermis by an enlarged base and is innervated from the suboesophageal ganglion; in form it is conical, lenticular, or foliaceous. From their histological structure and changes during the intermoult period, Gabe shows that the Y organs are comparable to the thoracic endocrine glands of holometabolous insects, and he suggests that they have something to do with moulting. Following this suggestion, Echali r (1954) made experimental tests by removing the organs. He found that bilateral ablation of the glands, when not made too late after they had already discharged their secretion, resulted in a very great lengthening of the intermoult period, far in excess of the usual time between moults. Echali r, therefore, contends that the Y organs are crustacean endocrine glands for the control of moulting. That they do not disappear in the adult as do the thoracic glands of insects, Gabe points out, follows from the fact that the crustaceans continue to moult in the adult stage.

I. EVOLUTION OF THE ARTHROPODS

In any discussion of arthropod metamorphosis the question of recapitulation always comes up in relation to the larval forms. If there is any ancestral recapitulation in ontogeny, it then becomes necessary to have at least a theoretical concept of the evolution of the arthropods and some idea of what ancestral forms they had that might be recapitulated in the development of the individual.

The evolutionary origin of the arthropods is hidden in remote Pre-Cambrian times, so probably we shall never know the facts from visual evidence. There is, however, ample evidence from a study of modern forms to indicate that the early progenitors of the arthropods were closely related to the progenitors of the annelid worms, and that these two groups of annulate animals had a common ancestor. The fundamental characters preserved in the annelid-arthropod organization are: an elongate segmented body, an alimentary canal extending through the length of the body, a paired ventral nerve cord with segmental ganglia, a somatic musculature, and mesodermal coelomic sacs. We may therefore visualize the primitive annulate as a very simple, wormlike creature having these features. The mode of development was anamorphic, new segments being formed in a subterminal zone of growth. From this primitive segmented worm the annelids have been directly evolved with little addition other than the development of segmental groups of lateral bristles, which in the polychaetes have been carried out on movable lateral lobes of the segments, the so-called parapodia, that serve for swimming and burrowing.

By a different type of specialization for locomotion, members of another branch from the ancestral stock developed ventrolateral, lobelike outgrowths of the body segments, and thus became walking animals. These primitive legs eventually evolved into the jointed appendages of modern arthropods, the lobelike origin of which is still recapitulated in the embryo. At the lobopod stage of evolution (fig. 1 A) the animals resembled a modern onychophoran, and are

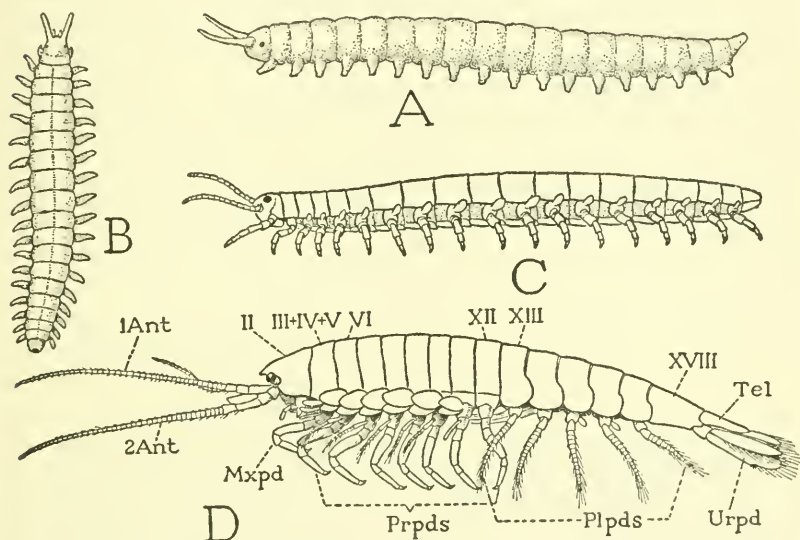


FIG. 1.—Theoretical evolutionary stages of the arthropods.

A, a primitive lobopod, common ancestral form of the Onychophora and Arthropoda. B, a derived form with longer and slenderer legs. C, a primitive arthropod with sclerotized integument, jointed legs, and gill lobes on the coxae. D, a fairly generalized modern crustacean, *Anaspides tasmaniae*.

1Ant, first antenna; 2Ant, second antenna; Mxpd, maxilliped; Plpds, pleopods; Prpds, pereopods; Tel, telson; Urpd, uropod; II-XVIII, body segments.

perhaps represented by such fossils as the Pre-Cambrian *Xenusion* and the Cambrian *Aysheaia*. The modern Onychophora are probably direct descendants from these early lobopods, and have structurally not progressed much beyond them. Others, however, acquired a sclerotization of the integument, which allowed the legs to become longer and slenderer (B), and finally jointed (C) for more efficient action in locomotion. These jointed-legged forms were the first true arthropods. The segmentation of the legs early took on a definite pattern, which has been preserved in both fossil and living arthropods, most of which retained the walking mode of locomotion, though some may also swim or fly.

From these early Pre-Cambrian arthropods (fig. 1 C) in which all the appendages were fully segmented ambulatory legs, the trilobites branched off by specialization of the body structure, but with no essential differentiation of the appendages. In the other derivative groups, however, the appendages took on different forms adapting them to various uses, but the number retained for walking is characteristic of the several modern arthropod groups. The myriapods use most of their postoral appendages for progression; the Malacostraca (D) use five or more pairs for walking, except where some of these have been modified for grasping; *Limulus* and the arachnids use four pairs, the insects three. That the ambulatory limbs, when limited in number, should in all cases be those of the middle part of the body, though not necessarily the same appendages, follows from the mechanical necessity of balance. The anterior appendages become sensory and gnathal in function; those of the abdomen have been modified for various purposes, such as respiration, silk spinning, copulation, egg laying, or swimming.

The modern arthropods comprise two distinct groups, the Chelicerata and the Mandibulata. In the chelicerates the first postoral appendages are a pair of pincerlike chelicerae that serve for feeding, and the ancestors of this group were probably closely related to the ancestors of the trilobites. The principal feeding organs of the mandibulates are a pair of jaws, the mandibles, formed of the second postoral appendages. The Mandibulata, including the crustaceans, the myriapods, and the insects, are certainly a monophyletic group, but their origin and their interrelationships are obscure.

Among the Crustacea the malacostracan type of organization (fig. 1 D), in which the thoracic appendages are typically ambulatory and the abdominal appendages natatory, would appear to be more primitive than the entomostracan types because it more closely conforms with the structure of other arthropods, and could be more directly derived from that of a primitive walking arthropod (C). The entomostracan forms, therefore, have been secondarily reconstructed for a purely pelagic life by a readaptation of the thoracic appendages for swimming.

If we accept the premise that the original arthropod (fig. 1 C) was a simple animal with jointed legs along the entire length of a uniformly segmented body, the crustaceans were derived from this common arthropod ancestor by specializations that established the generalized crustacean structure (D). Developmental recapitulation of adult crustacean structures, therefore, can go back only to the beginning of adult crustacean evolution. The embryo, however, starts its development from a single cell and the free larva completes development

up to the adult. The embryo and the early larva, therefore, represent pre-crustacean stages of arthropod evolution. The embryo, however, must reproduce its parental form. Hence the crustacean characters appear at a very early stage of ontogeny, but the resulting embryonic or larval stages are not recapitulations of adult crustacean evolution. The crustacean characters are simply precociously imposed on the anamorphic stages of ontogeny. Finally, if the embryo is set free as a larva at an early stage of development, it must be structurally adapted to a free life, and in its subsequent growth other adaptations may be necessary. Thus it comes about that metamorphosis still further complicates the course of ontogeny. The life histories of parasitic larvae best demonstrate that larval forms are metamorphic adaptations to a way of living, since the nonparasitic adult ancestors of such species can hardly be supposed to have had the larval form. Where a specialized adult structure has arisen since the crustaceans became crustaceans, there may be a true recapitulation of an earlier adult form, as in the megalops of the crabs. A further discussion of the nature of larval forms will be given in connection with the life history of a penaeid (p. 54).

II. THE NAUPLIUS AND THE METANAUPLIUS

Since among the crustaceans the young hatch at different periods of development, the youngest larvae may have very diverse forms in the various orders, representing different ontogenetic stages according to the degree of development they undergo within the egg. The earliest hatched larval form is the *nauplius*, which is particularly characteristic of the Entomostraca, but occurs also in the Euphausiacea and Penaeidea among the Malacostraca. The nauplius is usually followed by a *metanauplius*, which is the first stage of postembryonic growth. From the metanauplius on, development may be merely a matter of regular anamorphic growth by the successive addition of new segments and appendages, but in many species the larva takes on different forms as it develops. These ontogenetic changes differ so much in the various orders that no general description can be given, hence a discussion of them will be left to the next section of this paper. Special attention, however, must be given to the nauplius and the metanauplius.

The nauplius.—The nauplius is a minute creature, highly variable in form in different species, but typically ovoid or pyriform in shape with the larger end anterior (fig. 2 A). It has a pair of uniramous antennules, or first antenna (*1Ant*), typically biramous second antennae (*2Ant*) and mandibles (*Md*), and a median eye of two or more parts.

The antennae serve for locomotion. The internal organization includes usually an alimentary canal, a muscular system, a nervous system, and a pair of antennal excretory glands. The alimentary canal when fully developed consists of an endodermal mesenteron and an ectodermal stomodaeum and proctodaeum. The mouth is concealed above a large labrum; the anus is usually formed at a later stage. The nervous system includes three pairs of ganglia corresponding to the appendages. Though there is no visible segmentation in the ectoderm, the presence of appendages and ganglia shows that the nauplius is at

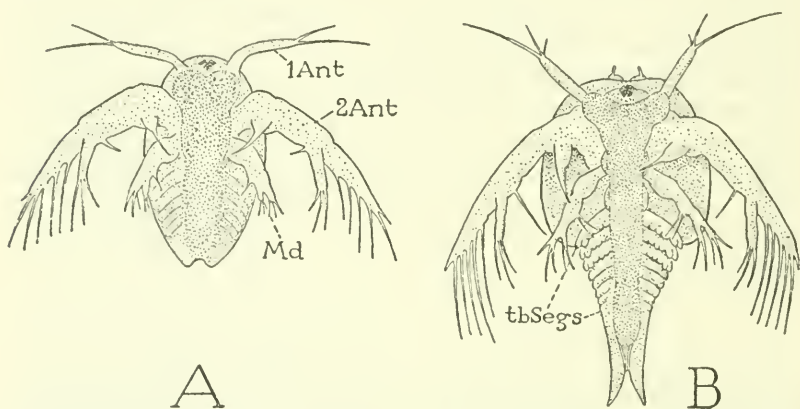


FIG. 2.—Nauplius and metanauplius of *Apus cancriformis* Bosc (from Claus, 1873).

A, nauplius, with first antennae (1Ant), second antennae (2Ant), and mandibles (Md), rudiments of teloblastic appendages seen through cuticle. B, metanauplius, appendages of teloblastic segments (tbSegs) exposed after first moult.

least a partly segmented stage of development. The region of the body behind the mandibles is that in which later the other segments will be formed, and their rudiments may be seen beneath the naupliar cuticle. When these segments are formed, however, they are generated by a different method from that which formed the anterior segments.

The nauplius is derived from a very early stage of embryonic development, represented in species that hatch at a later period by a simple embryo with rudiments of three pairs of appendages. The embryo still in the egg at this stage is clearly more simple in its structure than is the nauplius. The nauplius, therefore, is not merely an early hatched embryo—it has undergone a metamorphosis before hatching to adapt it to a free life in the water.

Our chief interest in the nauplius is the question of its theoretical value in phylogeny. The nauplius has been likened to the polychaete trochophore, and has been regarded as representing a primitive ancestral form of the Crustacea. The trochophore, however, is entirely unsegmented and does not have the internal organization of the nauplius. Later it becomes segmented by a direct division of the posterior part of its body into a few primary somites. Likewise the very young trilobite, known as a protaspis, at first shows no sign of segmentation, but it soon becomes marked by transverse grooves that divide it into a few primary segments corresponding with the segments in the prosoma of the adult. A similar early direct segmentation occurs also in the ontogeny of the Xiphosurida. The nauplius, therefore, would appear to represent the same stage of primary segmentation in crustacean ontogeny, though metamerism has not yet affected the ectoderm. It is reasonable then to infer, as contended by Iwanoff (1928), that the first somites in both the annelids and the arthropods were formed directly in the previously unsegmented body of the animal. The later extension of the body took place by the teloblastic generation of secondary somites from a subterminal zone of growth. The annelid and arthropod ancestors did not diverge until this method of anamorphic growth was fully established.

While the three larval forms discussed above do have a basic similarity of structure, which is primitive, it is evident that distinctive characters of more recent phylogenetic evolution have been impressed separately on each. The protaspis shows distinctly the definitive trilobite type of structure, the nauplius is clearly a crustacean, the trochophore is a young worm. The trochophore and the nauplius, moreover, are adapted in quite different ways for swimming at an early ontogenetic stage. The trochophore is not an adult ancestral form of the annelids, nor is the nauplius an ancestral form of the Crustacea.

The metanauplius.—The nauplius is the direct product of embryonic development. The further growth of the larva, or of the embryo if hatching occurs at a later stage, proceeds from a subterminal *zone of growth*, which becomes active before the naupliar cuticle is shed, so that rudiments of the new segments may be seen in the posterior part of the body of the nauplius (fig. 2 A). In the metanauplius (B), which appears after the last ecdysis of the nauplius, the posterior part of the body is much lengthened; it is now distinctly segmented and bears the rudiments of several pairs of new appendages. The postmandibular somites are the teloblastic segments (*tbSegs*).

Most studies that have been made on the larval development of Crustacea describe and picture the newly forming postnaupliar somites and appendages as they appear externally, without giving any information as to how they are formed. A paper by Fränsemeier (1939), however, describes the segment formation in the free-swimming metanauplius of the branchiopod *Artemia salina*, and papers by Sollaud (1923) and by Manton (1928, 1934) give details of the corresponding segmentation in the embryos of *Leander*, *Hemimysis*, and *Nebalia*.

In the anterior part of the nauplius the embryonic ectoderm is already differentiated into the tissues derived from it, and the mesoderm has been formed from the embryonic mesoblasts. The ectoderm of the body region behind the mandibles, however, is still undifferentiated and there is here no mesoderm distinguishable at this stage. At the posterior end of the body of *Artemia* the ectoderm forms a circumanal fold, the cells of which are the *ectodermal teloblasts* that will form the ectoderm of the new segments. From the ectodermal teloblasts, according to Fränsemeier, cells are given off into the interior of the body that become the *mesodermal teloblasts*, which will generate the secondary mesoderm. The naupliar mesoderm and the postnaupliar mesoderm of *Artemia* are thus distinct in their origin, though the formation of the second takes place 10 to 15 hours before the hatching of the nauplius. The teloblasts constitute the zone of growth, from which the new segments will be generated forward. The first segments formed from the teloblasts are said by Fränsemeier to be those of the first and second maxillae. As other segments are generated the anus-bearing region is carried posteriorly as a permanent telson. The proliferation zone remains active until the last segment is formed, when it is fully exhausted. The alimentary canal apparently simply lengthens posteriorly, the proctodaeum having been formed in the nauplius.

In the young naupliar embryo of the palemonine *Leander*, as described by Sollaud (1923), the postmandibular part of the body is a small anus-bearing lobe, or caudal papilla, which subsequently lengthens and projects free from the body in front of it and bends forward. A transverse row of large cells becomes differentiated in the ectoderm of the lobe before the anus, and later encircles the lobe. These cells are the ectodermal teloblasts. Below and a little before them is formed a corresponding ring of mesodermal teloblasts, which, according to Sollaud, are derived from the blastopore. The teloblasts generate the secondary segments in the usual manner, but in *Leander*, Sollaud says, the two maxillary segments are formed directly in the

larval body and not from the teloblasts, the first teloblastic segment being that of the first maxillipeds. In the Pericarida, however, he says the boundary between the primary tissue and the secondary tissue is between the segment of the mandibles and that of the first maxillae.

The accounts given by Manton (1928, 1934) of the embryonic process of secondary segmentation in *Hemimysis* and *Nebalia* are essentially the same as those of Sollaud for the embryo of *Leander* and of Fränsemeier for the larva of *Artemia*. Manton agrees with Fränsemeier that the teloblastic segments include both maxillary segments. In *Hemimysis*, she says, the naupliar and postnaupliar mesoderms are at first some distance apart, but later the teloblastic ectoderm and mesoderm extend forward as far as the first maxillary segment inclusive. The teloblasts of *Nebalia* are differentiated at the sides of the posterior blastoporic area, and the ectodermal teloblasts eventually form a complete circle around it. The mesodermal teloblasts, according to Manton, in agreement with Sollaud, are formed from the mesendodermal mass at the blastopore; Fränsemeier says they are proliferated from the ectodermal teloblasts. The ectodermal teloblasts, according to Manton, join the naupliar ectoderm between the mandibular and first maxillary segments, so that "all segments between the mandibular segment and the telson are formed by the teloblasts." The rudiment of each segment arises from one transverse row of descendants from the original ectodermal and mesodermal teloblasts. When the last abdominal segment is completed the teloblasts disappear in both *Hemimysis* and *Nebalia*.

Since the teloblastic generation of secondary somites added to the primary segmented body of the young larva or embryo is characteristic of the annelid worms and recurs in many of the arthropods, it must have been a way of lengthening the body developed in the very primitive wormlike ancestors of the two groups. The annelids and the arthropods, therefore, did not diverge until this method of growth was well established. Elsewhere the writer (1938) has suggested that telogenesis may have originated as a means of increasing the reproductive function by distributing the germ cells from the zone of growth through a larger number of segments.

III. EXAMPLES OF CRUSTACEAN METAMORPHOSES

The metamorphoses of Crustacea are so diverse that in a brief review of the subject we can include only a few examples representative of some of the principal orders. Since crustaceans that hatch at an early stage of ontogeny go through anamorphic phases of development

by the successive addition of segments and appendages, many of their changes are merely those resulting from the anamorphic manner of growth. In nearly all cases, however, there is some degree of metamorphosis superposed on the anamorphic stages, varying from a mere adaptation of the appendages for swimming to a total reconstruction of the animal for a parasitic way of life. The most striking examples of crustacean metamorphosis, therefore, occur in parasitic species. Among the Crustacea metamorphosis evidently has been developed separately in each order, and often independently in different members of the same order. There is no type of metamorphosis characteristic of large groups of orders, as in the holometabolous orders of insects. Moreover, since crustacean metamorphosis affects the juvenile anamorphic stages, except where it is carried over into the adult, the metamorphosis of Crustacea has no relation to that of the epimorphic insects. A brief but interesting account of the life-history problems of crustacean larvae is given by Gurney (1926).

For much assistance in preparing this section of the paper the writer is indebted to Dr. Fenner A. Chace, Jr., and his associates in the division of marine invertebrates of the U. S. National Museum.

BRANCHIOPODA

The branchiopods undergo few changes during their larval development that are not the result of simple anamorphic growth by which the body and the appendages are completed and brought to the adult condition through successive instars. The branchiopods are thus of interest in showing a simple progressive development from nauplius to adult, which is accompanied, however, by a specialization of the postgnathal appendages for swimming. As an example we may take the life history of *Branchinecta occidentalis* Dodds as described by Heath (1924).

The newly hatched larva of *Branchinecta* is a typical nauplius (fig. 3 A) with three pairs of appendages, a median simple eye, and a large labrum, but the oval, unsegmented posterior part of the body is more than usually constricted from the forepart. The large second antennae are the principal swimming organs. Between the nauplius and the second instar, or metanauplius (B), a very considerable change takes place. Lateral compound eyes are now conspicuous by their pigmentation. The posterior part of the body has greatly lengthened, and bears rudiments of maxillulae, maxillae, and six or seven following pairs of appendages. In the third instar (C) the post-maxillary appendages have lengthened and the more anterior pairs

have taken on a leglike form; their mesal margins are indented, and each limb bears a conspicuous lobe, or flabellum, just proximal to an apical point. The body is more lengthened behind the appendages and

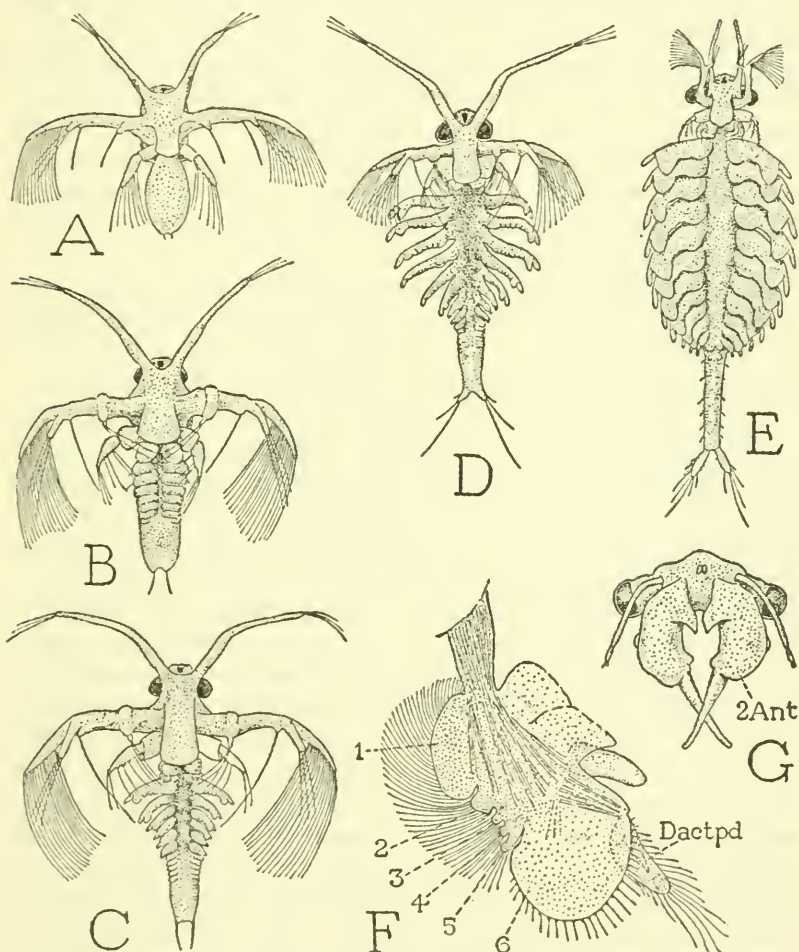


FIG. 3.—Branchiopoda. *Branchinecta occidentalis* Dodds, developmental stages (from Heath, 1924) and a thoracic limb of the adult.

A, newly hatched nauplius, length 0.4 mm. B, second instar. C, third instar. D, fifth instar. E, eighth instar, 2.9 mm. F, sixth left thoracic limb of adult male, with six endites (1-6) and a movable terminal lobe (*Dactpd*). G, head of adult male, anterior, with large second antennae (*2Ant*).

shows lines of further segmentation. After two more moults, the larva in the fifth instar (D) reaches an average length of 1.6 mm. The second antennae are relatively much shortened, but the legs have

increased in length and are more distinctly indented on their mesal margins. The slender posterior part of the body bears rudiments of four new appendages, and its apex is split into a pair of small caudal lobes. The postmaxillary appendages continue to develop through the sixth and seventh instars until 11 pairs are present. In the eighth instar (E) they have lost their leglike form and have become broad flat phyllopodia with large flabella and slender apical lobes. At this stage, as the thoracic appendages take over the swimming function, the second antennae are much reduced in size and are directed forward. Heath enumerates 17 instars in the larval life of *Branchinecta*, but development beyond the eighth instar merely brings about refinements toward the adult structure.

The larval stages of *Artemia* described by Heath (1924) are very similar to those of *Branchinecta*, as are those of *Branchipus* described by Oehmichen (1921). In the Concostraca and Cladocera the larval development is complicated by the formation of a bivalved shell.

The development of the branchiopod appendages is of interest because it suggests that the natatory phyllopodium has been evolved from a segmented ambulatory leg. The mature appendage of *Branchinecta* (fig. 3 F) is cut on its mesal margin into a number of lobes, of which five (1-5) are commonly described as endites, while the large, so-called flabellum (6) is interpreted as the endopodite, and the movable apical lobe as the exopodite. The same structure is seen in the limbs of *Branchipus* (fig. 27 A, B) and other anostracans. Since endites in general are lobes of the limb segments, the six mesal lobes of the phyllopodium suggest that they represent six leg segments, coxopodite to propodite. The movable, independently muscled apical lobe (*Dactpd*), therefore, should be the dactylopodite. There is thus in the phyllopodium evidence of the presence of the seven segments characteristic of the crustacean walking legs. In the second maxilliped of *Apus* (fig. 27 C) seven segments, including a terminal dactylopodite, are plainly evident, and each of the first six segments except the ischiopodite bears an endite. We can hardly escape the conclusion, therefore, that the phyllopodial limbs of the branchiopods have been evolved from 7-segmented walking legs. The metamorphosis of the appendages, therefore, has taken place since the crustaceans became crustaceans, and is recapitulated in the larval ontogeny. A more extensive discussion of the nature of the primitive arthropod limbs is given in section IV of this paper.

About the only metamorphosis in the life history of *Branchinecta* is the temporary adaptation of the antennae for swimming. It is hardly to be supposed that the primitive crustaceans swam with their

antennae. The nauplius has only three pairs of limbs, and, since it must swim, it has no choice but to use what appendages it has. As the body lengthens and the postmandibular appendages become broad and flat, these appendages assume the function for which they were modified in the branchiopod ancestors. The antennae then revert to a more simple form (fig. 3 E), and in the adult they are again modified, in the male (G) for grasping.

OSTRACODA

The ostracods, being enclosed in a bivalve shell from the time they leave the egg, go through no body changes of form that might be termed a metamorphosis; their appendages, however, give an impressive example of the extreme degree of structural modification that an ordinary segmented leg may take on.

The newly hatched ostracod larva is in the nauplius stage of development (fig. 4 A), since it has only the three usual pairs of naupliar appendages. It is not a typical nauplius, however; the antennae and mandibles are uniramous, and the body is already enclosed in a shell formed in the egg. Here is a good demonstration, then, that the crustacean nauplius, in addition to its primitive features, can take on a specialized structure characteristic of the order to which it belongs. During the postnaupliar stages, as shown in the series of drawings (fig. 4) here copied from Schreiber (1922) on the development of *Cyprinotus incongruens*, the postmandibular appendages are successively added until the definitive number of seven in all is present in the eighth instar (F), in which the larva has attained essentially the adult structure.

There is no question that the naupliar appendages are the antennules, the antennae, and the mandibles, but there has been some difference of opinion as to the identity of the postnaupliar appendages. In the Cypridae the first appendage after the mandible (fig. 5 B, 4) bears a large, flat, fringed lobe projecting upward in the shell cavity, and this appendage is commonly regarded as the maxilla. The next appendage (5) Schreiber termed the maxilliped. These two appendages on each side in *Cypris* arise side by side on the arm of the hypostome (D, 4, 5), and Cannon (1926) regarded them as the maxillula and the maxilla, respectively. In *Limnocythere inopinata* (A), however, as in other Cytheridae and in Nesideidae, appendage 5 is a typical leg well separated from 4. If, therefore, appendage 4 is interpreted as the maxilla, appendages 5, 6, and 7 are thoracic legs, and Kesling (1951) says this is now the accepted interpretation of

the ostracod limbs. Since we are here not particularly concerned with the identification of the appendages, they have simply been numbered on the drawings for purposes of comparison.

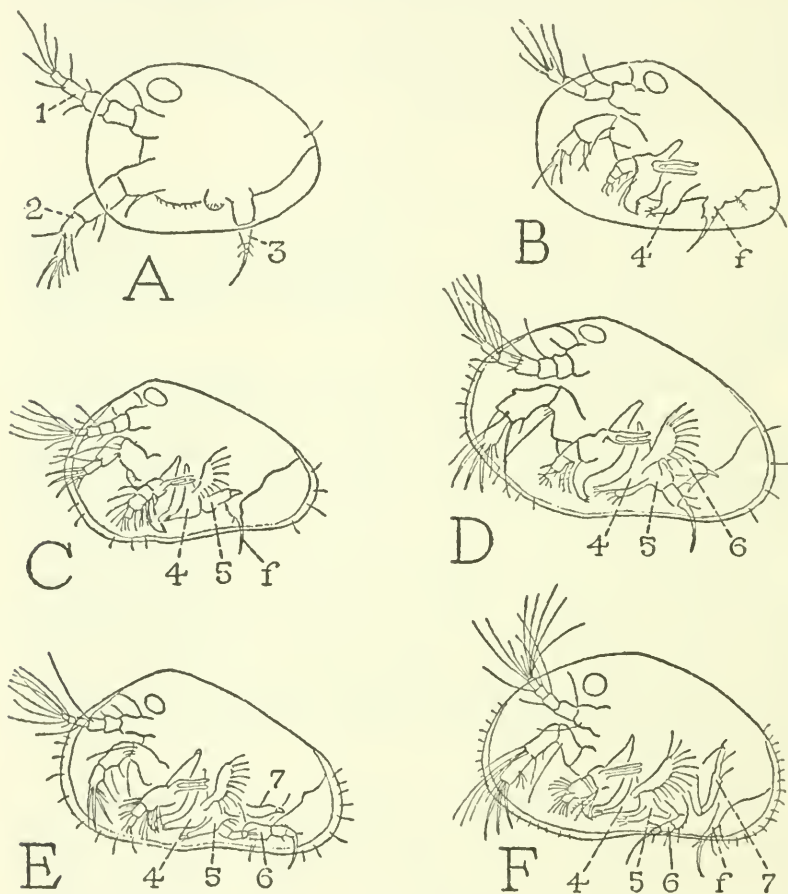


FIG. 4.—Ostracoda. Larval stages of *Cyprinotus incongruus* Ramdohr (from Schreiber, 1922).

A, nauplius, with three pairs of appendages. B, second instar, with one pair of added appendages (4) and caudal furca (f). C, fourth instar, with fifth appendages (5). D, fifth instar, with sixth appendages (6). E, sixth instar, with seventh appendages (7). F, eighth instar, essentially adult structure.

Inasmuch as in such forms as *Limnocythere* (fig. 5 A) the antennae and the last three pairs of appendages have the form of segmented legs, and in *Cypris* (B) the sixth and seventh appendages are typical legs (E), it may be inferred that the primitive ostracod appendages

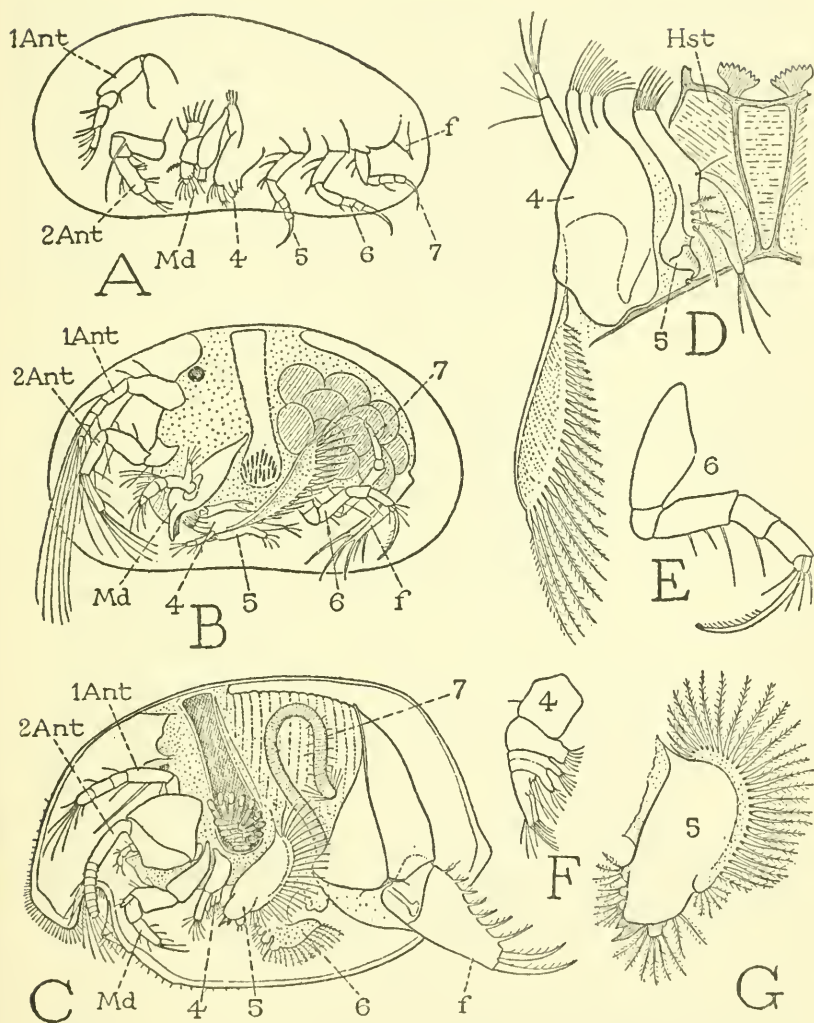


FIG. 5.—Ostracoda.

A, *Limnocythere inopinata* (Baird), eighth instar (from Scheerer-Ostermyer, 1940). B, *Cypris testudinaria* Sharpe, adult, left shell removed. C, *Philomedes globosa* (Lilljeborg), adult, left shell removed. D, *Cypris testudinaria*, fourth and fifth appendages of left side and hypostome (Hst), posterior. E, same, sixth appendage. F, *Philomedes globosa*, fourth appendage. G, same, fifth appendage.

were all ambulatory limbs. Moreover, since the legs of *Limnocythere* can be correlated with appendages of a very different structure in other genera, the ostracods give an actual demonstration of the changes that legs can undergo in adaptation to new uses. The very unleglike fifth appendage of *Cypris* (D, 5), for example, must have been evolved from a typical leg such as its representative in *Limnocythere* (A, 5). This same appendage in *Philomedes* (C, 5) is again quite different from the corresponding appendage in *Cypris*. The maxilla of *Cypris* (D, 4) is represented in *Philomedes* (C, F, 4) by an appendage still suggestive of its leg origin. The fifth appendage of *Philomedes* (C, G, 5), however, has no resemblance to its counterpart in *Limnocythere* (A, 5), though the presence of three small marginal lobes and an apical tooth might be taken as evidence of a former segmentation. The sixth appendage (C, 6) has likewise three small marginal lobes and a broad, fringed apical lobe, but otherwise it has departed far from the structure of a leg (A, 6). The seventh appendage of *Philomedes* (C, 7) has lost all semblance of a leg; it has become a long, flexible, vermiform cleaning organ armed with an apical brush of recurved bristles. The corresponding appendage in *Cypris* (B, 7) is likewise used for cleaning the shell chamber, but the only concession it has made to its function is an inversion of position. The sixth appendage of *Cypris testudinaria* (fig. 5 E) looks like a typical 7-segmented crustacean limb, counting the long terminal claw as the dactylopodite. The fourth and fifth podomeres of this appendage, however, are perhaps not true segments, since in *Cypridopsis vidua* Kesling (1951, fig. 20) shows that the muscles from the sixth podomere have their origins in the base of the fourth podomere.

The ostracods give no support to the theoretical phyllopod origin of crustacean limbs, and show clearly how simple segmented legs can be modified into very unleglike structures.

COPEPODA

The copepods include marine and fresh-water free-swimming species and a large number of parasitic species. They are nearly all very small crustaceans, mostly from 0.50 mm. to 10 mm. in length in the adult stage. The simpler free-swimming copepods seem to approach more closely the typical shrimplike form of the higher crustaceans than do any of the other entomostracans. The body of a generalized form such as the marine *Calanus* (fig. 6) is divided into a cephalothoracic region bearing the appendages, and a slender limbless abdomen. The cephalothorax includes an anterior unsegmented part

(*H*) known as the head, or cephalosome, and a posterior thoracic region of five segments. The head carries the two pairs of antennae, the mandibles, two pairs of maxillae, and the first pair of legs, or maxillipeds. The five segments of the thoracic region bear each a pair of legs, but the legs of the last pair may be much reduced. The genital ducts open on the basal segment of the abdomen.

The free-swimming copepods occur in such vast numbers in the ocean and in some inland lakes that they constitute a most important food source for many other aquatic animals from arrowworms to whales, but particularly for fishes. Being minute creatures themselves, the free copepods feed on the microscopic plant life of the water,

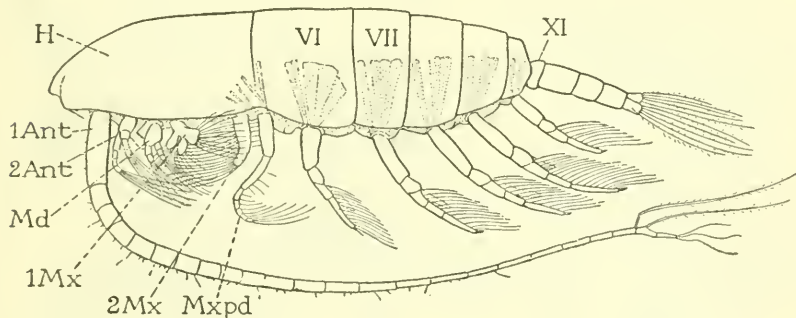


FIG. 6.—Copepoda. *Calanus cristatus* Kröyer, adult.

1Ant, first antenna; 2Ant, second antenna; *H*, "head"; *Md*, mandible; 1Mx, first maxilla; 2Mx, second maxilla; *Mxpd*, maxilliped; *VI*, *VII*, *XI*, body segments.

which, elaborated in their own bodies, is thus passed on as food for the larger animals. It would seem, however, that the copepods have retaliated on the animals that eat them, since many species have become parasites of their potential enemies. Though fish are their favorite hosts, the parasitic copepods are not discriminative and attack almost every kind of creature that lives in the ocean. On the other hand, the copepods themselves are infested by numerous parasites, even by some of their own kind. Evidently life in the ocean is not a happy existence for either the predators or their victims.

The nonparasitic copepods go through no changes of form in their life histories that can truly be called a metamorphosis. Their environment is practically the same at all periods of their lives, and there is no call for adaptive modifications in either the larval or the adult stage. The successive developmental stages are merely steps in growth from youth to maturity. As an example, we may take the fresh-water

Cyclops and follow its life history as described by Dietrich (1915) and by Ziegelmayer (1925).

The *Cyclops* larva hatches from the egg as a typical nauplius (figs. 7 A, 8 A), which is followed by a second nauplius instar and four metanaupliar instars (fig. 8 B, C, D, E) in which the body lengthens, and finally (E) five pairs of appendages are added beyond the mandibles, including the maxillipeds (*Mxpd*) and two pairs of legs (*1L*,

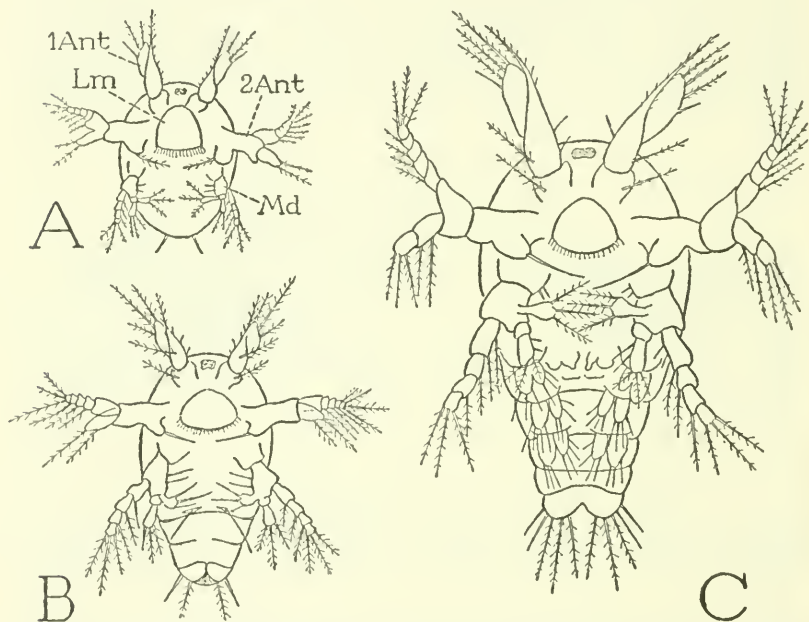


FIG. 7.—Copepoda. Nauplius and two metanaupliar instars of *Cyclops* (outlines from Ziegelmayer, 1925).

A, nauplius, ventral, showing three pairs of appendages and labrum (*Lm*). B, first metanaupliar instar. C, fourth metanaupliar instar.

2L). At the next moult the larva (F) begins to take on the form and structure of the adult (G) and is now termed a *copepodid*, the ending *id* signifying that at this stage the larva has become copepodlike. The first copepodid acquires a third pair of legs; with further growth it passes through six copepodid instars until at last it becomes a sexually mature adult (G). Among *Cyclops* species there is thus no abrupt change between the various stages of growth, but new segments are added and the appendages develop from simple rudiments to their definitive forms. According to Ziegelmayer the segments formed after the nauplius stage are generated in a subterminal zone of growth.

The genus *Calanus*, a typical free-swimming marine copepod of the suborder Gymnoplea, likewise develops from nauplius to adult by ordinary anamorphic growth without any metamorphic changes

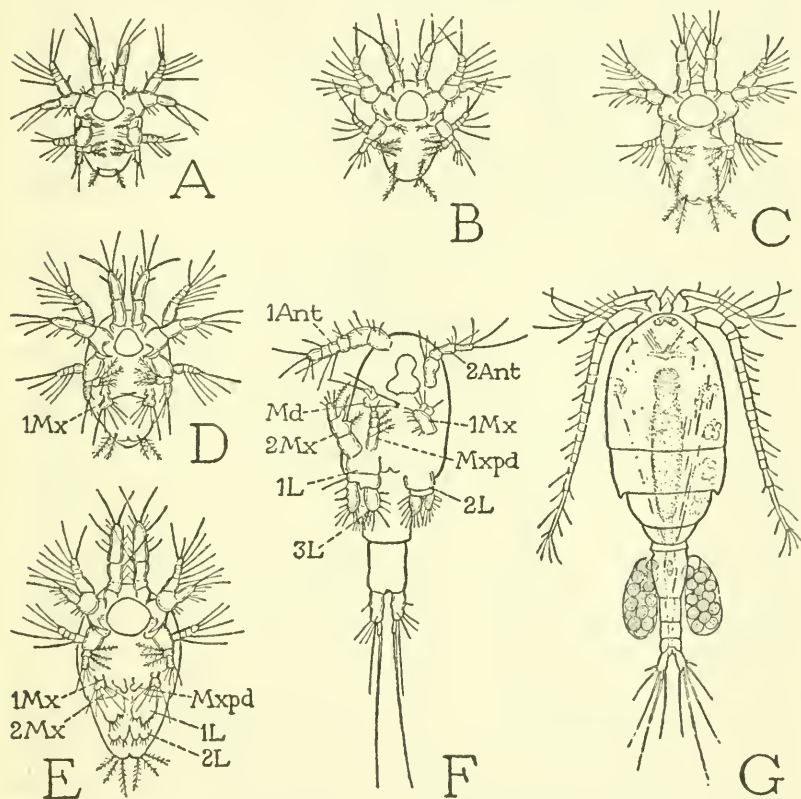


FIG. 8.—Copepoda: Podoplea. Developmental stages and adult of *Cyclops*. (A-F from Dietrich, 1915; G from Claus, 1863).

A, *Cyclops strenuus* Fischer, nauplius, 0.119 mm. B, same, first metanauplius. C, same, second metanauplius. D, same, third metanauplius. E, same, fourth metanauplius. F, same, first copepodid, 0.303 mm. G, *Cyclops coronatus* Claus, adult female with eggs, 3.50 mm.

1Ant, first antenna; 2Ant, second antenna; 1L, 2L, 3L, legs; Md, mandible; 1Mx, 2Mx, first and second maxillae; Mxpd, maxilliped.

adaptive to different ways of living at different stages. The life history of the common *Calanus finmarchicus* has been described by Lebour (1916). The first six instars the author calls nauplii, but some of them would ordinarily be regarded as metanauplii, since two posterior segments and indications of a third segment are said to appear in the

fifth stage, with traces of the fifth and sixth pairs of appendages. In the sixth instar, judging from related species, there are present second maxillae, maxillipeds, and two pairs of swimming legs. The next instar is that of the first copepodid, which has three pairs of legs; the fourth legs appear in the second copepodid instar, and the definitive number of five is present in the third copepodid. The fifth and last copepodid is essentially like the adult. The free-swimming copepods, therefore, have a typical anamorphic development. Being crustaceans, they are primarily constructed for life in the water, and so long as they maintain a free existence there is no need of metamorphic adaptations to any other way of living.

When now we turn to the parasitic copepods, the story is very different. An aquatic animal that hatches as a freely swimming larva and then becomes sedentary on another animal from which it extracts its food changes its environment and its mode of living in a very radical way. In some manner difficult to understand metamorphic changes of structure have been evolved that adapt the parasitic animal to its life of parasitism, and in many cases the transformation has been carried so far that the adult parasite could not be identified, or even recognized as a crustacean, if its early stages were not known.

A few copepods appear to be transitional in their habits between a free life and one of parasitism. Such species are termed semiparasitic by Wilson (1921b), who says they are found on worms, mollusks, echinoderms, and in the gill chambers of crabs. These species are capable of swimming freely in the water, and their residence on any one host may be temporary. Their mouth parts, according to Wilson, are not suitable for either chewing or sucking and appear to be adapted for licking nourishment from the animals to which they attach themselves. A species with biting mouth parts, however, could hardly resist sampling the blood of its host and then becoming an habitual parasite.

The truly parasitic copepods include a large number of species, all of which undergo striking metamorphic adaptations to the nature of the host or the part of the host attacked, and some of them lead a double life on two different species of hosts. Some parasitic copepods undergo their metamorphoses during the larval development and become again free living in the adult stage; others remain on the host and attain their highest degree of metamorphosis as adults. Most of them, however, hatch from the eggs as typical nauplii, and in this stage or the following copepodid stage they must find their proper hosts.

As an example of the life history of a parasitic copepod that returns to a free life in the adult stage, we may take the monstrillid *Cymbasoma rigidum* Thompson, described by Malaquin (1901) as *Haemocera danae* (Claparède), which in its larval stages lives in the blood vessel of the serpulid worm *Salmacina dysteri* Huxley. The nauplius (fig. 9 A) has the usual three pairs of naupliar appendages, but the mandibles are recurved hooks, and the young larva has no mouth or alimentary canal. It is poorly fitted for swimming, and Malaquin suggests that the females probably sow their eggs over a colony of the serpulids. When in contact with a worm the nauplius attaches itself by its mandibular hooks to the worm's integument, but it has no special organs for penetration. The skin of the worm, however, is delicate, and, a puncture once effected, the nauplius does a most surprising thing; it casts off its own cuticle and its appendages and forces its soft nude body into the host. Within the latter it becomes a shrunken, oval mass of undifferentiated cells (B), as if it had returned to an early embryonic condition to begin development all over again. In this form the parasite traverses the coelom of the host and makes its way into the ventral blood vessel. Here it secretes a new cuticle and then from its ventral side anteriorly there grow out two tapering, armlike processes (C) that extend posteriorly in the blood vessel of the worm and will serve the parasite as food-absorbing organs. Here, therefore, we see a metamorphic development adapting the parasite to its life in the host that certainly had no counterpart in the presumed free-living ancestors of its species. It is hard enough to believe the facts themselves, and we can speculate in vain as to how they all came about in evolution. The nauplius is prepared in advance for the life it is to lead by being provided with hooked mandibles, but what induces it to shed its cuticle and appendages and to squeeze itself into the worm?

With the growth of the young larva in the worm (fig. 9 H) the nutritive arms increase in length (D, E), the new cuticle is drawn out into a rostrum in front (E, R), and on the enlarged conical posterior part of the body it becomes armed with circles of spines directed forward. The organs of the future adult now gradually develop within the cuticle of the larva (F), and the abdomen forms as a ventral flexure (*Ab*) of the posterior part of the body. At an early stage the first antennae are regenerated (F, G, *1Ant*) and eventually penetrate into the rostrum (I) when the head tissue has receded from the latter. From this point on the parasite develops normally into the adult form within the cuticular sheath of the larva. Finally, when its development is almost completed (I), the parasite becomes strongly

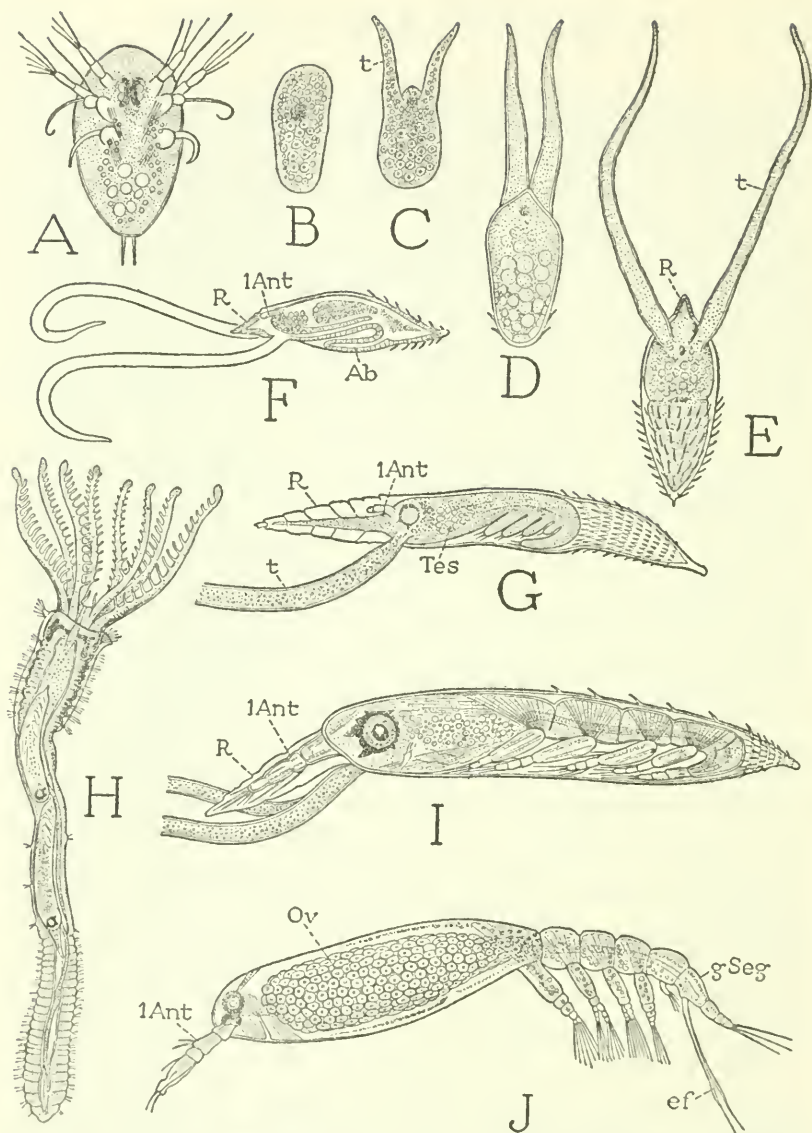


FIG. 9.—Copepoda: Monstrillidae. Larval stages and adult of *Haemocera danae* (Claparède) parasitic in the polychaete *Salmacina dysteri* Huxley (from Malaquin, 1901).

A, free nauplius. B, after penetration into host. C, same, with nutritive tentacles (*t*). D, same, later stage. E, later stage, with cuticular envelope, rostrum (*R*), and spines. F, beginning transformation to adult inside cuticular sheath, rudiment of abdomen (*Ab*) bent forward. G, later stage of male, showing testis (*Tes*). H, specimen of *Salmacina* with two parasites in ventral blood vessel. I, male parasite almost adult. J, adult female, free after shedding the sheath and leaving the host; *1Ant*, first antenna, *ef*, egg filaments, *gSeg*, genital segment, *Ov*, ovary.

active, doubling and straightening upon itself with the result that it ruptures both its enclosing sheath and the integument of the host. Then it escapes, leaving behind in its late host its spiny cuticle and its nutritive arms, which will no longer be needed. The monstrillid thus, according to Malaquin, makes during its life only two moults, one on entering the host, the other on leaving it. With its liberation the adult becomes at once an active free-swimming copepod (J). It now has only one pair of antennae and four pairs of swimming legs, and it lacks a complete alimentary canal. The body of the female, however, is mostly filled with a great mass of eggs (J, *Ov*); the business of the adult is the procreation of more parasites.

Members of the family Caligidae, mostly parasitic on fish, are also free in the adult stage, but, though the adults are at liberty to leave the host and are equipped with swimming legs, they still depend for their food on the host that nourished them as larvae or on some other fish of the same kind. They, therefore, live largely as free external parasites. The structure and habits of many species of Caligidae have been described by Wilson (1921a), and a detailed account of the larval stages of *Caligus curtus* (O. F. Müller) is given by Heegaard (1947).

In *Caligus curtus*, according to Heegaard, there are two naupliar instars, the second of which goes over directly into a first copepodid without an intervening metanaupliar stage. The first copepodid is followed by a second copepodid, and then come five larval stages in a form known as a *chalinus* before the individual becomes adult. The actively swimming first copepodid has the responsibility of finding a host, which will be a codfish. It grasps a scale or a fin ray of the fish by means of its clawed second antennae, and holds on with the maxillipeds. After attachment the copepodid moults into the second copepodid (fig. 10 A). In this stage a gland in the head produces a secretion which will be discharged from the frontal region as a filament (B), which becomes firmly fixed to a scale or a fin ray of the host. The parasite now becomes quiescent and takes no food as it hangs motionless on its attachment line, while within its cuticle a development takes place that will transform the copepodid into the first *chalinus*. This quiescent period of the copepod (B) is termed by Heegaard and some other writers a "pupa," but, though motionless and nonfeeding, it is not comparable to the pupa of an insect. The insect pupa is a stage in itself during which the metamorphosed larva reverts to the parental form. Each larval instar of any arthropod begins its development within the loosened cuticle of the preceding instar. The copepod "pupa," therefore, is merely the second copepodid

after completion of its own growth when the first chalimus is developing beneath its cuticle. An insect larva in a corresponding stage becomes quiescent and ceases to feed, but it is not a pupa. This concealed period in which any instar begins its development within the

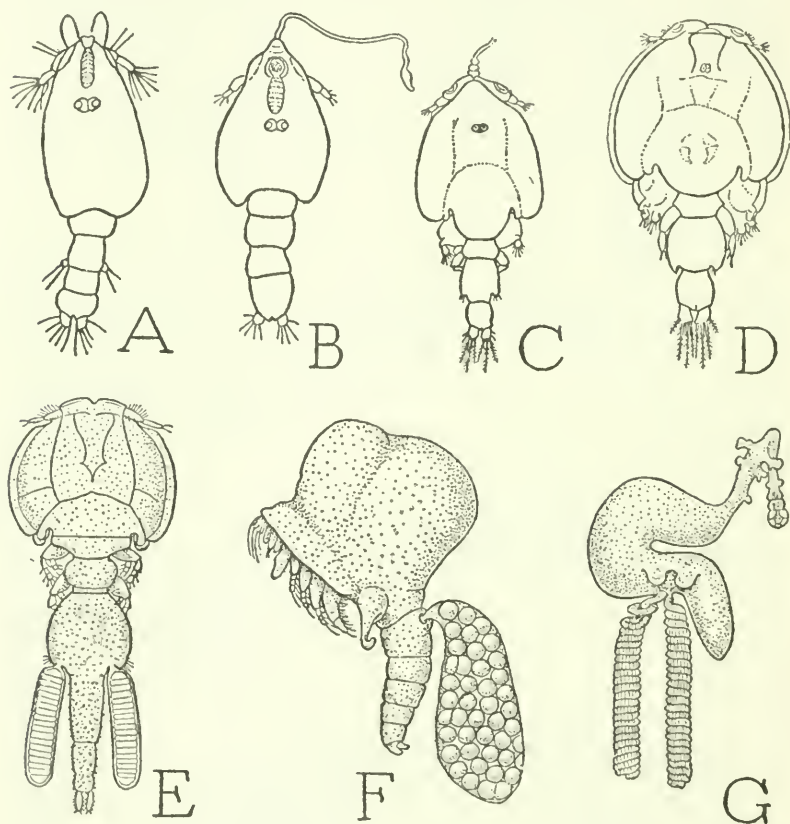


FIG. 10.—Copepoda. Larval and adult stages of fish parasites. (A, B from Heegaard, 1947; C, D from Wilson, 1905; E, F from Wilson, 1921a; G from Wilson, 1917.)

A, *Caligus curtus* (O. F. Müller), second copepodid. B, same, transforming stage of second copepodid. C, same, mature male chalimus. D, same, adult male. E, *Trebius latifurcatus* Wilson, adult female. F, *Blakeanus corniger* Wilson, adult female. G, *Haemobaphes cyclopterina* (Fab.), adult female.

cuticle of the preceding instar has been termed by Hinton (1946) the *pharate*, or cloaked, phase of development.

The young chalimus that emerges from the copepodid cuticle is not particularly different from the copepodid, though it is somewhat more advanced in development. Its first concern is to reattach itself to the

host, since the old filament remained with the discarded copepodid skin. Heegaard (1947) gives an interesting account of how the young chalimus with the pointed frontal lobe of its head bores a hole in a fin ray of the host. Into the wound thus formed is injected the secretion from the head gland, which hardens and holds fast, while the chalimus backs away and draws it out into a filament that secures the parasite to the host, but still allows it to move about on its tether. According to Heegaard each of the four succeeding chalimus stages reattaches itself in the same manner. The chalimus (C) was given its name because when first discovered it was thought to be the adult of an unknown species. Since the chalimus stages progressively develop from the second copepodid to the adult (D), they evidently represent the later copepodid stages of free-living copepods.

The adults of *Caligus curtus* (fig. 10 D) have pretty much the form and structure of an ordinary copepod, but, having no attachment to the host, both the males and the females are free to swim away. The egg-carrying female of another species with similar habits is shown at E of the figure. Since these copepods are dependent on a host for food in the adult stage, they retain their parasitic habits and are generally found crawling and feeding on the host, though they have not become specially modified in structure for a life of parasitism. This condition of dependence on a host, however, Wilson (1915) points out, constitutes the first step toward adult degeneration. If the adult parasite finds it advantageous to remain on the host, organs of locomotion become unnecessary, and in the end all that is needed are organs of nutrition and reproduction. The species shown at F, parasitic in an ascidian, still retains its appendages and a segmented abdomen, but the thorax has taken on a strange shape. The female at G, however, a permanent parasite on the gills of a fish, has degenerated from the copepod structure almost to the limit of simplification. Yet, as already noted, "degeneration" is merely adaptation by the elimination of unnecessary organs.

An example of an intermediate degree of degenerative simplification is seen in the lernaepodid fish parasite *Achtheres ambloplitis* (fig. 11) described by Wilson (1911). In this copepod, Wilson says, the naupliar and metanaupliar stages are completed in the egg, and the larva hatches as a copepodid (A). During the egg stage the head gland produces a filament, which is still coiled in the head of the emerging copepodid (A, f). The young larva has two pairs of feathery swimming legs, and its maxillipeds (*Mxp d*) are armed with strong hooks. It swims actively in search of a host, which must be a fish of the surface-swimming Centrarchidae. That the young copepod

deliberately presents itself to the head end of a fish has perhaps not been observed, but the fish unwittingly engulfs the copepod as food, which is of course just what the prospective parasite wanted it to do. To save itself from being swallowed the copepod grasps a gill arch of the fish with the hooks of its maxillipeds. Then it pushes its head into

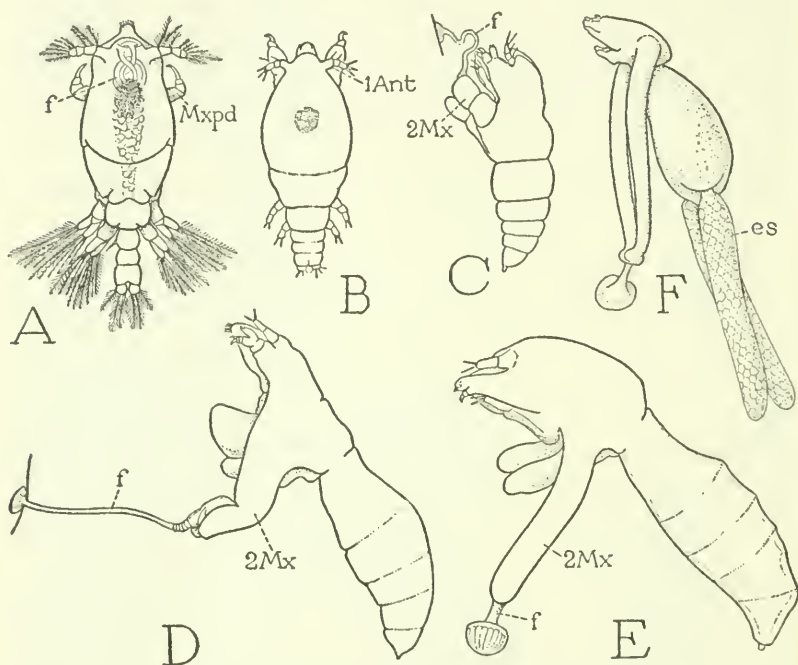


FIG. 11.—Copepoda: Lernaeopodidae. Developmental stages of fish parasites (from Wilson, 1910, 1915).

A, *Achtheres ambloplitis* Kellicott, first copepodid, with filament (*f*) in head. B, same, second copepodid. C, same, with filament extruded and attached. D, same, adult male. E, same, adult female. F, *Salminicola siscowat* (Kellicott), egg-carrying female.

the soft skin of a gill, which act breaks the cuticle over its head and releases the filament. The filament protrudes into the wound of the gill and the end spreads out into a disc that anchors the parasite inside the gill chamber of the fish.

The first copepodid larva of *Achtheres* (fig. 11 A) undergoes a moult and enters a second copepodid instar (B), which is decreased in size and has taken on a different shape. The swimming legs, being now useless organs, are greatly reduced and later disappear (C). The mandibles have become toothed piercing organs for feeding. The

large second maxillae (C, $2Mx$) are much thickened and securely grasp the base of the attachment filament (f) by means of hooks imbedded in apical depressions. Then the larva backs away and draws the filament out to its full length, and thus maintains its hold on the gill with sufficient freedom of movement for feeding. At the next moult the sexes are mature. The female grows to a length of 4 or 5 mm., but the male remains a pygmy not over 1 mm. long.

In the adult female (fig. 11 E) the maxillae are greatly lengthened, but the filament (f) is contracted so that only a short stalk projects beyond the maxillae. The maxillae of the male (D) are relatively not so long as those of the female, but the filament is unshortened. The filament, being a product of an internal head gland, is not shed and renewed at the moults; it retains its attachment and thus allows the parasite to complete its life in security within the gill chamber of the fish. The long filament of the small adult male permits the male to swing around on his tether until he comes in contact with a female, whom he grasps with his maxilliped claws and then lets go his hold on the filament, which remains attached to the gill. The female of another similar species of the genus *Salminicola* (F) is depicted by Wilson (1915) carrying her extruded eggs (es) in two long cylindrical sacs projecting from the gonopores while still attached to the gill of the fish. The newly hatched young presumably are carried out of the gill chamber in the expiratory currents of water.

A good example of a parasitic copepod that inhabits two hosts during its life is the well-known fish parasite *Lernaeocera branchialis* (L.), a member of the Lernaeopodidae. This species during its larval life is an attached parasite on the gills of a flounder, but when adult both the male and the female become free and leave the flounder. The male undergoes no further transformation, and, after mating with a female still on the flounder, his purpose is accomplished. The female, on the other hand, is not yet sexually mature, and some instinct now urges her to leave the flounder and to seek a cod on which to complete the development of her ovaries. Once attached in the gill chamber of a cod she goes through an adult metamorphosis by which she is functionally reduced to the bare essentials necessary for feeding and egg production. For an account of the life history of *Lernaeocera branchialis* we may draw on the work of Pedaschenko (1898), Scott (1901), Wilson (1917), Schuurmans-Stekhoven (1936), Sproston (1942), and Capart (1948).

There is some difference of opinion concerning the nature of the early forms of this species. Pedaschenko says the first larva is a metanauplius (fig. 12 B); Scott and Sproston observed only one early

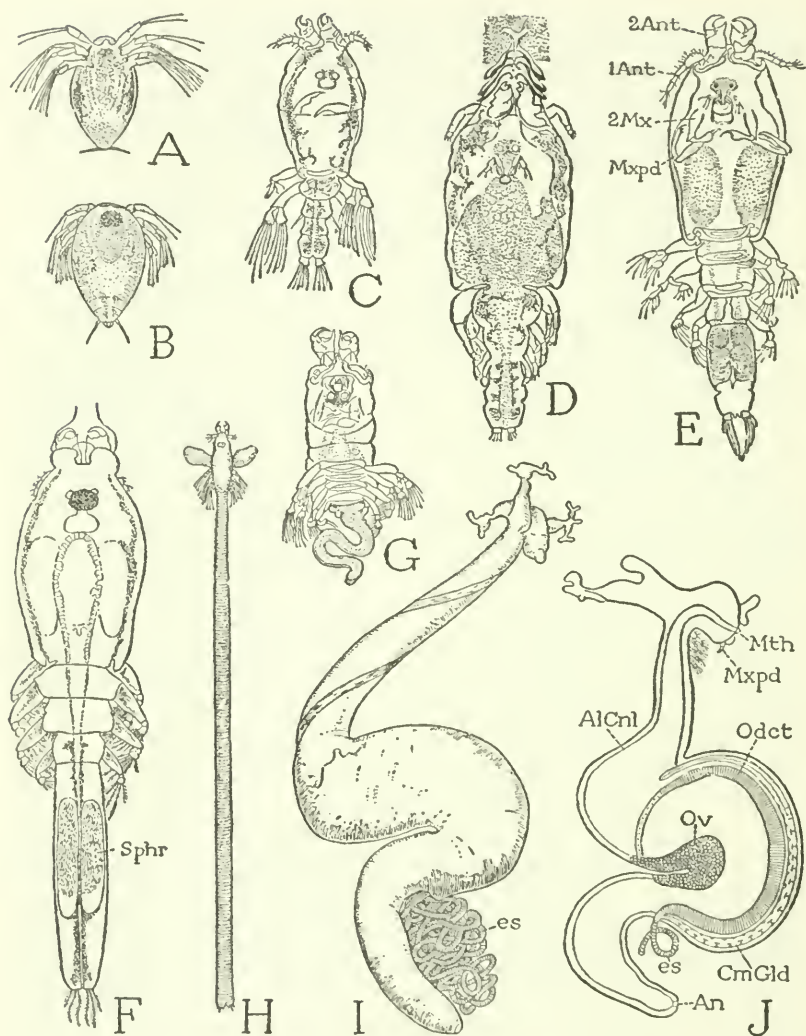


FIG. 12.—Copepoda. Developmental stages of the fish parasite *Lernaeocera branchialis* (L.). (A, C, D, E, G from Sproston, 1942; B from Pedaschenko, 1898; F, I from Capart, 1948; H, J from Scott, 1901.)

A, nauplius, 0.37 mm. B, metanauplius. C, free-swimming copepodid. D, third instar of chalimus stage on flounder. E, free-swimming adult male, 1.55 mm. F, young inseminated female on flounder. G, female on cod, beginning metamorphosis to penella stage. H, female in fully developed penella stage. 11.4 mm. I, adult egg-carrying female on cod, 40 mm. J, section of mature female.

An, anus; AlCnl, alimentary canal; 1Ant, first antenna; 2Ant, second antenna; CmGld, cement gland; es, egg string; Mth, mouth; 2Mx, second maxilla; Mxpd, maxilliped; Odct, oviduct; Ov, ovary; Sphr, spermatophore.

stage, and called this stage a nauplius (A) ; while Wilson and Capart record both a nauplius and a metanauplius. The matter is of no particular importance for us in a study of the metamorphosis of the species. Whatever the larva that hatches from the egg may be, it moults into a free-swimming copepodid (C). Though the copepodid is only about half a millimeter in length, it has the responsibility of finding a flounder and of fixing itself to the gills of the fish, for which latter purpose it is provided with strongly chelate second antennae. Its hold on the gill, Sproston says, is never relinquished, and becomes the anchorage of the parasite until the free-swimming adult stage is reached. The gill filaments, however, are grasped also by the second maxillae in order to bring the mouth parts into close contact with the tissues on which the parasite feeds.

When the copepodid moults the larva becomes a chalimus (fig. 12 D), but there is little change in form or structure. The chalimus, however, in its first instar acquires an additional attachment on the host in the form of a filament secreted by a gland in the head, which is anchored in the gill by two diverging branches that penetrate into punctures in the gill tissue. The rest of the secretion from the gland, Sproston says, falls back on the head of the larva where it hardens into a conical hood. The chalimus goes through four instars, and with each moult but the last a new hood is formed while the old ones remain, so that there are thus formed a set of overlapping caps corresponding in number with the moults. The third instar of the chalimus, to be identified as such by its three hoods, is illustrated at D of figure 12, redrawn from Sproston. The copepodid and the chalimus are metamorphic larval forms adapted to their respective functions of swimming and parasitic feeding. During its four instars the chalimus gradually approaches the adult structure, which is attained at the fourth moult after the copepodid stage.

The adult male of *Lernaeocera* (fig. 12 E) leaves the old attachment filament with the castoff chalimus cuticle hanging on the gill of the flounder, and goes off in search of a female. The female (F), however, awaits the coming of a male before she relinquishes her hold on the flounder. When the male finds a female still attached, mating takes place ; two large spermatophores are inserted into the genital ducts of the female and are eventually lodged in her lengthened genital segment (F, *Sphr*). The female, still not sexually mature, then frees herself from the flounder and swims away to look for her second host, which should be a cod. On attaining a prospective victim, the female fixes herself to the bases of the gills by her second antennae, and now begins her metamorphosis into the final egg-producing stage.

After attachment on the cod the head of the female undergoes a curious transformation. Large branching, hornlike processes grow out from it and sink into the host tissue as anchoring devices (fig. 12 I). The proboscislike mouth region penetrates deeply in the flesh at the base of the gill until a large blood vessel is reached, from which the female will draw a rich nourishment for the maturing of her eggs. The first change of the body is a lengthening of the abdomen, principally the genital segment, which grows out in a twisted wormlike form (G), and finally (H) becomes a long, straight, slender appendage hanging from the thorax. At this stage the female is known as a penella from her resemblance to another adult copepod of that name. In the figure the penella stage shown at H is, of course, drawn on a much smaller scale than is the female at F or G. Next, the abdomen swells into a great, elongate, twisted bag (I). The female in her final stage is said by Wilson (1917) to attain a length of 40 millimeters when fully extended. From now on she is merely an egg-producing organism. Her internal organs (J) consist principally of the enlarged alimentary canal (*AlCanl*), the ovaries (*Ov*) and oviducts (*Odct*), and a pair of cement glands (*CmGld*) that form the casings for the eggs. The eggs are discharged in two long coiled strings (*es*), which, Wilson says, reach a length of 150 to 200 millimeters. Considering the number of eggs that the species produces, any flounder or cod may consider itself lucky if it escapes infestation. According to Schuurmans-Stekhoven there is only one generation of the parasite each year.

The metamorphosis of *Lernaeocera branchialis* affects principally the female on the secondary host. The less modified chalimus instars carry on the developmental processes while attached on the flounder as do the copepodid stages of free-living species. The adult male and the adult female on leaving the flounder are normal, swimming copepods. The transformation of the female on the cod involves, on the one hand, a simplification of the thorax until it becomes indistinguishable from the abdomen, except for the retention of the appendages; but, on the other hand, there is a new development of anchoring process on the head, and a great overgrowth of the reproductive part of the body. The metamorphosis of the female, therefore, is both recessive and progressive in an anatomical sense. A study of the development and metamorphosis should take into consideration not only the anatomical changes that the individual goes through, but also the changes in its instincts. The copepodid of *Lernaeocera*, for example, must have an instinctive urge to attach itself to a flounder; the adult female instinctively leaves the flounder and looks for a cod.

Copepod fish parasites are not all content with attacking the scales, fins, or gills of the host. Some make their abode in the nostrils of the fish; others penetrate through the skin into the body cavity where they attack the vital inner organs. The worst of them are members of the genus *Phrixecephalus*, several species of which are described by Wilson (1917). These parasites bore into the eyes of their victims in order to feed from blood vessels at the back of the organs. Parasites seem to have been endowed by nature with great versatility, but the life of a fish is nothing to be envied.

CIRRIPIEDIA

The cirripeds include the familiar barnacles and several groups of parasitic species. The first-stage larvae in most cases are nauplii usually characterized by the presence of a pair of lateral *frontal horns* on the anterior part of the body. In some species the horns are merely short spines (figs. 14 B, 16 A, *fh*), in others they are long and either straight or curved, but when present the horns identify the nauplius as a young cirriped. The nauplius becomes a metanauplius; the metanauplius transforms into a free-swimming larval stage known as a *cypris* because its body is enclosed in a bivalve shell with a closing muscle, and thus resembles the ostracod of the same name. The cirriped cypris (fig. 14 C) has six pairs of swimming legs, a simple median eye, compound lateral eyes, and a pair of antennules projecting from the anterior end of the shell. After swimming freely for some time the cypris of most species attaches itself by the antennules to some solid object on which it remains permanently fixed and here develops into the adult form.

The barnacles in the adult stage (fig. 14 F, H) are sedentary on rocks, clam shells, wooden piles, ship bottoms, whales, or almost anything else in the ocean, and they get their food from the water. The parasitic cirripeds attach themselves to other animals and derive their sustenance from the host. The adult barnacles retain enough of their ancestral structure to be recognized as crustaceans; some of the parasitic cirripeds, on the other hand, undergo such extreme degrees of adult metamorphosis that their crustacean derivation is known only from their early larval stages.

The Ascothoracica.—The members of this suborder are of particular interest because as adults they appear to be equivalent to the cypris stage of other cirripeds. If they truly are cirripeds, therefore, they evidently are a primitive group of the order, and suggest that the cirripeds have been derived from cyprislike ancestors, perhaps re-

lated to the bivalved Ostracoda. From the standpoint of metamorphosis the Ascothoracica are of small interest, since whatever modifications some of them do undergo effect principally a simplification of the cypris structure. They are all minute creatures parasitic on Actinozoa and Echinodermata.

The least modified member of the Ascothoracica is *Synagoga mira* Norman (fig. 13 A), which lives externally on the black corals *Antipathes*, clinging to the host by the large antennules. Since *Synagoga* has well-developed setigerous legs, however, it appears probable that it can relax its hold and swim from one host to another. The species is known only from a few specimens described by Norman (1913). The head and thorax are enclosed in a large, oval bivalve shell, 4 millimeters in length, provided with strong adductor muscles, but the slender, five-segmented abdomen projects freely from the shell and bears a pair of long uropods. The large antennules (*Ant*) are armed with apical hooks; the six pairs of thoracic legs bear long setae and are evidently adapted for swimming. The mouth parts as described by Norman are slender piercing organs enclosed in a large conical proboscis (*Prb*). Of all the Ascothoracica, *Synagoga mira* alone appears to have no metamorphosis and to have retained the ability to swim; no other species, therefore, has so good a claim to being a primitive cirriped.

A related member of the Ascothoracica is described by Okada (1938) as *Synagoga metacrinicola* (fig. 13 B). This species has the entire body enclosed in the shell, the abdomen being relatively short, but otherwise it is similar to *S. mira*. Okada finds well-differentiated males and females in *S. metacrinicola*, the sexes being separate in most of the Ascothoracica, in which the males are much smaller than the females. He reports that Norman's specimens, supposed to be females, are found on reexamination by sections to be males with mature spermatozoa. Okada thus demonstrates that the known examples of *Synagoga* are adult forms and not larvae of an otherwise unknown species, as some writers had suggested they might be.

The other Ascothoracica that are parasitic on horny corals appear as small budlike bodies on the coral stems. The shells are of various shapes and in some species are enclosed in a tunic derived from the host. In most of these forms the legs are more or less reduced and lack swimming setae. An ascothoracid described by Heegaard (1951) as *Ascothorax bulbosa*, found in specimens of an ophiuroid, or brittle starfish, has an oval shell (fig. 13 C), the small males being attached dorsally on the females beneath the cuticle of the latter. The body

of the animal (D, E) is somewhat deformed and the thoracic legs are reduced.

The greatest modification among the Ascothoracica occurs in the

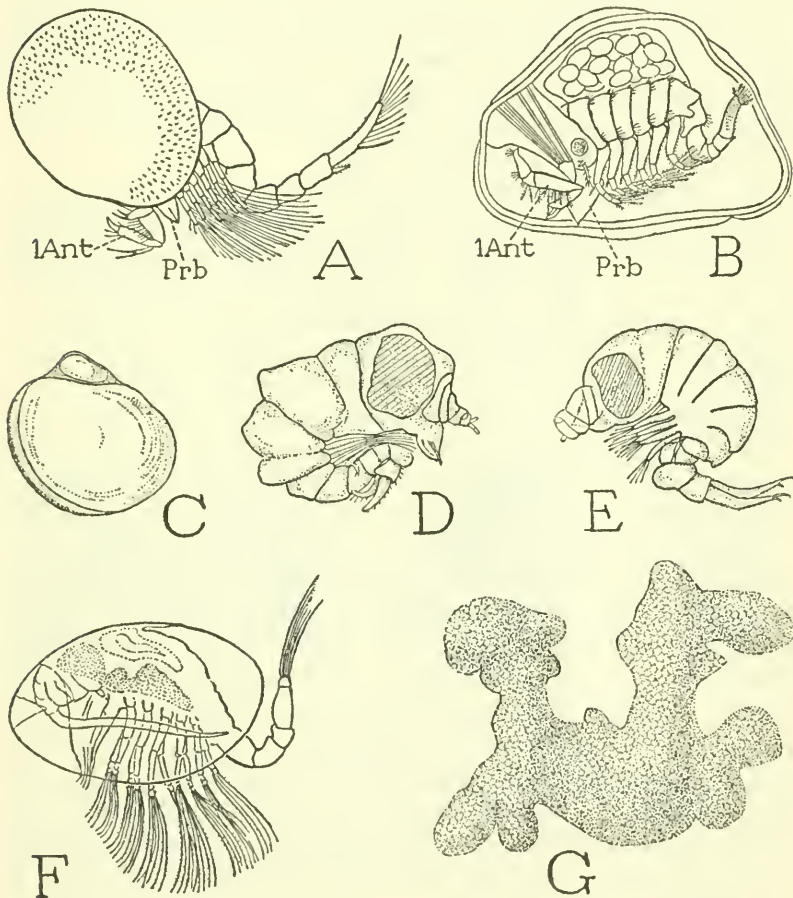


FIG. 13.—Cirripedia: Ascothoracica. (A from Norman, 1913; B from Okada, 1938; C, D, E from Heegaard, 1951; F, G from Knipowitsch, 1890.)

A, *Synagoga mira* Norman, adult. B, *Synagoga metacrinicola* Okada. C, *Ascothorax bulbosa* Heegaard, shell of female with small male on top, internal parasite of ophiuroid. D, same, female. E, same, male. F, *Dendrogaster astericola* Knipowitsch, cypris larva. G, same, adult enclosed in branched mantle, internal parasite of starfish.

Dendrogasteridae, which are internal parasites of echinoderms. *Dendrogaster astericola*, described by Knipowitsch (1890), is enclosed in a voluminous mantle (fig. 13 G) with large lateral lobes, which are penetrated by diverticula of the stomach. The cypris larva (F),

however, is a typical cirriped cypris, much resembling the adult of *Synagoga* (A). A species figured by Fisher (1911) as *Dendrogaster arbusculus*, found in a Californian starfish, has an elaborately branched structure.

The known nauplii of the Ascothoracica, according to Okada, differ from the nauplii of other cirripeds in the absence of the usual frontal horns, another feature that sets the ascothoracicans off as a primitive branch of the cirripeds. Some species hatch as nauplii, others as metanauplii, and still others in the cypris stage.

The Thoracica.—To this suborder belong the barnacles, which in the adult stage are enclosed in calcareous shells. Some are conical and sit flat on the substrate (fig. 14 F), others are flattened and supported on stalks (H). When either kind is broken open, however, there is exposed within the shell a shrimplike creature (G) lying on its back or standing on its head with its cirruslike feet, when active, sticking out of the top or side (H) with a waving movement.

The nauplius of a common barnacle such as *Balanus*, described by Runnström (1924-1925), has the typical naupliar structure (fig. 14 A) except for the pair of small horns (B, *fh*) on the anterior part of its body. Runnström describes two naupliar stages, but since the second becomes elongate and acquires rudiments of three postmandibular appendages it would ordinarily be called a metanauplius. After a few hours of swimming, the metanauplius abruptly transforms into a cypris (C) with a bivalve shell and long seta-bearing legs, wherewith it is better equipped for a pelagic life. Eventually the cypris fixes itself to a support by its first antennae (1 *Ant*), each of which (E) is provided with an adhesive cup on the third segment. A cementing substance discharged through the antennae from glands in the head gives the cypris a permanent attachment. Then the cypris withdraws the hind part of its body and its legs into the shell, and now begins the formation of the plates of the adult barnacle. According to Runnström, the plates are first formed as chitinizations of the mantle and only later become calcified. When the plates have the essential adult pattern (D) the cypris shell is cast off, and with the moult the legs of the cypris are replaced by the cirri of the barnacle.

The metamorphosis of the cypris into the barnacle is not excessive. It is a structural adaptation to the permanently sessile condition within the shell, and the eyes are absorbed as now useless organs. The changes that take place in the body have been described by Doochin (1951). The shell-closing muscle of the cypris is retained (fig. 14 G, *mcl*), and the mantle supporting the plates of the shell is attached to

the body only around the ends of the muscle. The peduncle of the stalked barnacles is a product of the head and becomes occupied by connective tissue and muscles. The barnacles are hermaphroditic, but they generally live in crowded colonies and cross fertilization is made possible by a long, tubular penis arising at the base of the vestigial abdomen.

The Rhizocephala.—In this suborder of parasitic cirripeds we encounter the strangest metamorphic phenomena known in the whole

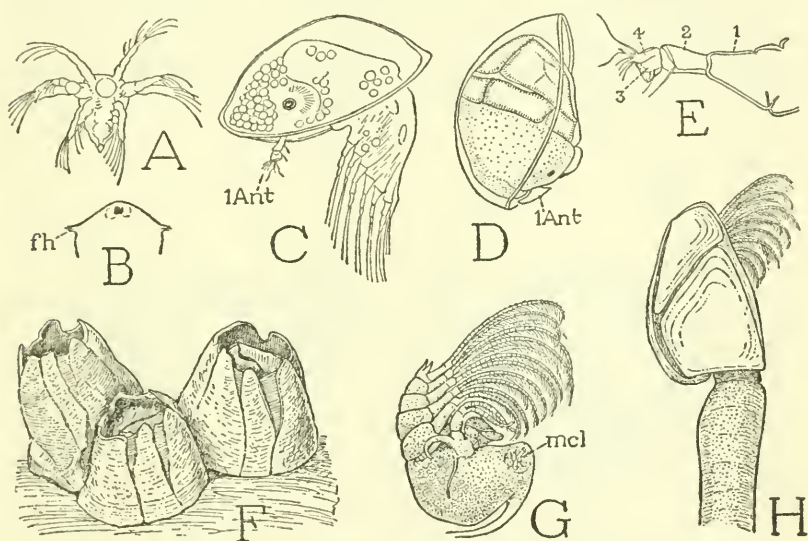


FIG. 14.—Cirripedia: Thoracica. (A-E from Runnström, 1924-1925.)

A, *Balanus balanoides* (L.), nauplius. B, same, anterior end of body with median eye and frontal horns (*fh*). C, same, cypris larva. D, same, later stage, barnacle plates formed inside cypris shell. E, same, first antenna of cypris with attachment cup on third segment. F, *Balanus eburneus* Gould, group of adults. G, *Lepas anserifera* L., adult animal in natural position removed from shell. H, same, stalked shell.

animal kingdom. The rhizocephalans include a number of genera, of which the best known are crab parasites of the genus *Sacculina*. The visible external evidence that a crab is parasitized by a sacculinid is the presence of a large saclike body attached ventrally on the crab at the base of the abdomen (fig. 15 A). This external sac is the reproductive part of the parasite containing the ovaries and the testes, but from it long, rootlike processes extend into the body of the crab and serve for the nutrition of the parasite. The eggs are fertilized and hatch within the external sac, giving rise to nauplii, which transform into typical cirriped cypris larvae. The free-swimming cypris

larvae escape through a hole in the sac, find another crab, and enter the latter after undergoing extraordinary transformation processes. The life history of *Sacculina carcini* Thompson was fully described and illustrated by Delage in 1884, and Delage's account has been verified, at least in part, by G. Smith (1906) and Veillet (1945). It still remains as the authentic history of a *Sacculina*, and the following story of the life and metamorphosis of this parasite is based on the papers by Delage and Smith, with illustrations taken from both.

The nauplius of *Sacculina* (fig. 16 A) has the characteristic frontal horns (*fh*) of cirriped nauplii, but it lacks an alimentary canal and has neither a mouth nor an anus. After several moults the nauplius becomes a cypris larva (B) with a length of 0.20 mm. On leaving

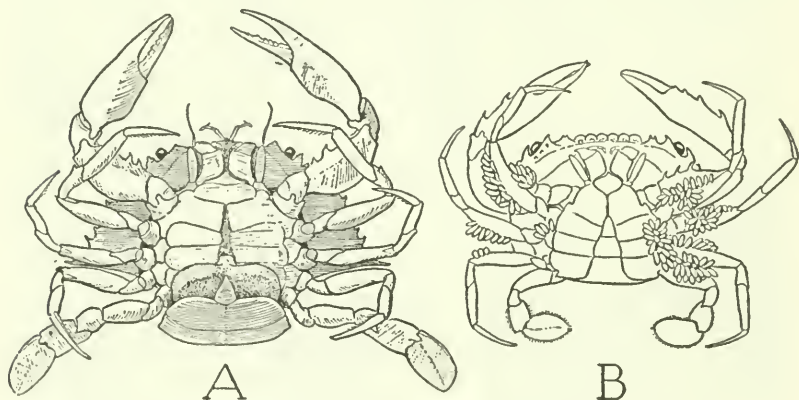


FIG. 15.—Cirripedia: Rhizocephala. External parasitic stages on crabs.

A, *Loxothylacus texanus* Boschma, a sacculinid on *Callinectes sapidus* Rathbun. B, *Thompsonsonia* on *Thalamita prymna* (Herbst) (from Potts, 1915).

the brood sac on the crab, the cypris leads a free life in the ocean for several days. Finally, on finding a young crab that has just moulted, it attaches itself to the latter by one of its antennules (*C*, *1 Ant*), which are provided with small suction cups. The point of attachment is usually in the membrane at the base of a hair (*Hr*). When firmly secured the cypris begins violent swinging movements of the body, which detach the thorax (*Th*) along with the legs and the abdomen and throw the whole rear part of the body out of the shell (*Sh*). From the large hole thus left in the head end of the cypris are now expelled most of the internal tissues, leaving only a mass of cells containing the reproductive elements. Later the hole closes.

While this process of elimination has been going on, other changes take place. The body of the larva separates from the shell (D) and contracts to a sac walled by the ectoderm, which is much smaller than

the original cypris (B). Soon a new cuticle is secreted on the surface of the sac (D, 1Ct) in continuity with the cuticle of the attached antenna, and the larva becomes a compact oval body still within the shell but now entirely free from it. Again, as if preparing for a moult, a second cuticle (2Ct) is formed beneath the outer one, and a small point (*d*) grows out from its anterior end into the hollow of the antenna. The body of the larva then retracts within the outer cuticle (E), and as it does so the cuticular point elongates into a long, hollow dartlike tube (*d*) with the narrow end cut off obliquely like the point of a hypodermic needle, and its widened base embedded in the body of the retracted tissue of the larva. This newly formed organ Delage called the *dart*, and the larva armed with the dart he termed a *kentrogon* (from Greek *kentron*, a dart, and *gonos*, a larva). The shell together with its loose inclusions is now thrown off, leaving the kentrogon, still enclosed in the outer cuticle, attached to the crab by the antenna (F).

The body of the larva again expands and pushes the dart into the antenna (fig. 16 F) until its tip comes into contact with the integument of the crab. Since the parasite is held fast by the antenna, the dart pierces the integument instead, pushing the larva away from it, and finally (G) projects into the body of the crab. Now the soft tissues of the larva contract away from the cuticle but remain still connected with the base of the dart. The remains of the larva thus have a free passageway into the body of the crab through the narrow channel of the dart, the orifice of which is said by Delage to be 3 to 6 microns in diameter. Though Delage says he did not observe the actual passage of the larval substance through the dart, globules are seen inside the dart and the parasite is next found inside the crab. By the method of the *Sacculina* a mouse might get into the pantry through the keyhole of the door, but once inside it would have to devise a new way of eating. This problem the *Sacculina* solves very easily—it simply adopts the feeding method of a plant by sending out absorbent roots among the organs of the crab.

Inside the crab the parasite becomes a small oval body consisting of a mass of cells enclosed in an ectodermal epithelium. It finds its way to the ventral side of the crab's intestine and here becomes attached. Now the principal concern of the parasite is to obtain nourishment from the host for maturing the germ cells which it has brought with it from the cypris stage. Incidentally, this will be the first food from an external source that the larva itself has had, since it was hatched without an alimentary canal. The larval body expands against the intestine of the crab (fig. 17 A) and sends out branching

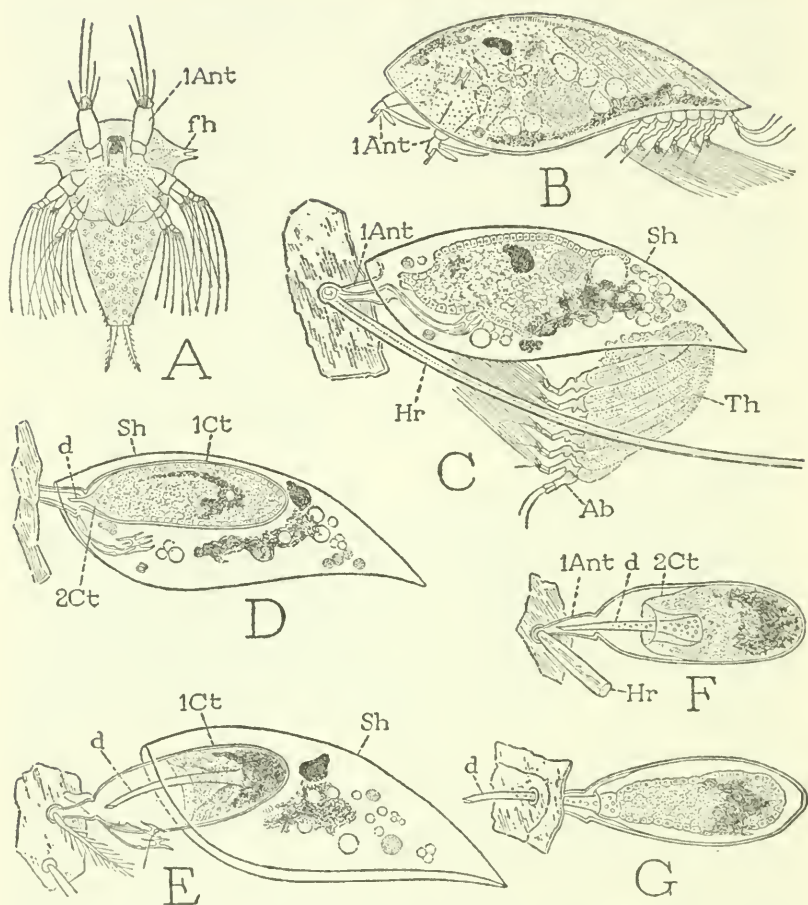


FIG. 16.—Cirripedia: Rhizocephala. Metamorphosis of *Sacculina carcini* Thompson (from Delage, 1884).

A, nauplius. B, free-swimming cypris stage ready to moult. C, cypris fixed by antenna at base of hair of crab, shell separated, thorax detached and thrown off with internal tissues. D, larva still in shell has formed a new cuticle (1Ct). E, shell being shed, larval body retracted within cuticle, with long, hollow "dart" (d) extended toward base of antenna. F, larva with a second inner cuticle (2Ct), the dart extended into antenna. G, larval body expanded, the dart has pierced the hair membrane of the crab.

Ab, abdomen; 1Ant, first antenna; 1Ct, outer cuticle; 2Ct, inner cuticle; d, dart; fh, frontal horn; Hr, hair of crab; Sh, cypris shell; Th, thorax.

rootlike processes (*rhizai*), which continue to grow, branch, and unite until a network surrounds the intestine (B), from which branches penetrate between the other organs and extend out into the appendages. The roots do not enter the tissue of the crab, but Delage says only the heart and the gills are not attacked. These are the organs necessary for maintaining the life of the host and therefore that of the parasite, but how did the parasite ever learn to discriminate? The *Sacculina* at this stage has been aptly likened to a fungus. That a crustacean can be so transformed shows the unlimited potentialities of metamorphosis.

When nutrition has been fully provided for, attention must be given to the reproductive function. If the eggs were allowed to hatch inside the crab, the young larvae would find themselves in a prison from which there would be no escape. The body of the parasite, therefore, emerges through the ventral integument of the crab and becomes a brood chamber in which the eggs mature and from which the larvae are liberated into the ocean. The pressure of the parasite's body causes a dissolution of the crab's epidermis beneath it, and prevents the formation of cuticle at this point. Consequently at the next moult of the crab the *Sacculina* body containing the reproductive cells emerges and becomes external, but is still connected with the crab by a short peduncle giving passage to the feeding roots. The place of emergence is at the middle of an abdominal segment; if it were intersegmental, movements of the abdomen might constrict the peduncle and shut off the food supply of the parasite. It seems that the simpler a creature may be in its organization, the more does nature guard it against emergencies. It is interesting to note that the species shown at A of figure 15 is exactly modeled to fit into the pocket between the under surface of the thorax of the crab and the reflexed abdomen beneath it.

The external parasite, as seen in section (fig. 17 C, D) consists of a central mass of cells contained in a tunic suspended from the peduncle, and of an outer mantle (*mn*) that encloses a peripheral brood chamber (*bc*). The figures at C and D, taken from G. Smith (1906), depict a species of *Peltogaster*, but the structure is essentially the same in *Sacculina*. The cells of the central mass are the eggs in the ovary (*Ov*); above them is a pair of tubular testes (*Tes*) and a single nerve ganglion (*Gng*). The ripe eggs are discharged into the mantle cavity and here fertilized by spermatozoa from the testes, the parasites being necessarily hermaphroditic. The larvae escape in the cypris stage from an opening (D, *op*) in one end of the brood chamber. Successive lots of eggs are discharged and fertilized, and after each brood of larvae the cuticular lining of the brood chamber

is shed. The maturation of the sperm and the eggs and the fertilization of the latter are fully described by Smith, but here ends our discussion of the metamorphosis of *Sacculina*.

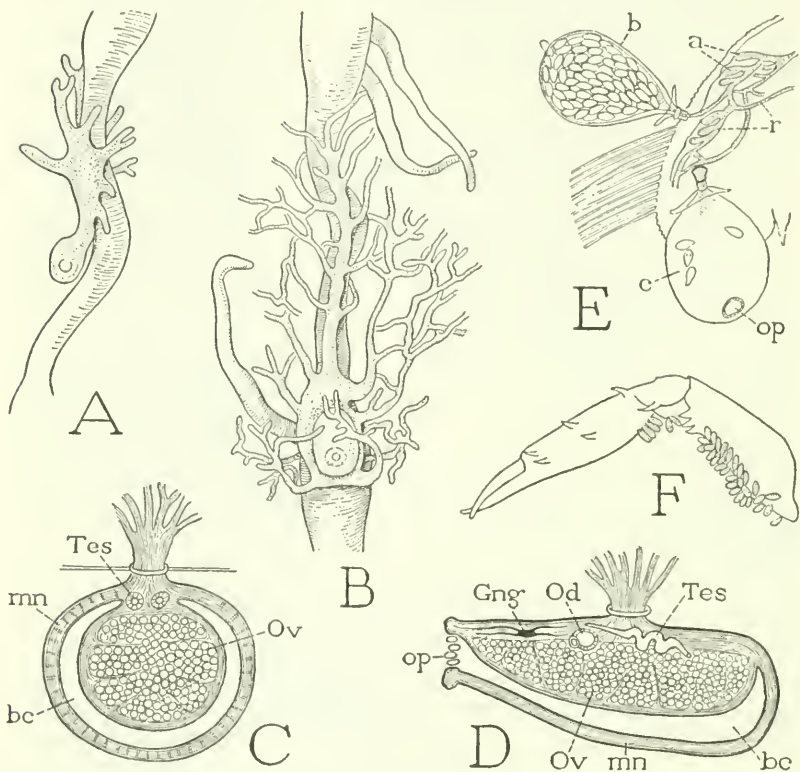


FIG. 17.—Cirripedia; Rhizocephala. Internal and external parasitic stages. (A-D from G. Smith, 1906; E, F from Potts, 1915.)

A, *Sacculina neglecta* attached on intestine of crab *Inachus scorpio*. B, same, later stage with root system developed. C, *Peltogaster* sp., diagrammatic cross section of parasite after emergence on ventral side of crab. D, same, longitudinal section. E, *Thompsonia* sp., part of root system in tail fan of crab *Synalpheus brucei*, with external brood sacs. F, same, external sacs on chela of *Thalamita prymna*.

a, internal reproductive buds; b, external brood sac containing cypris larvae; bc, brood cavity; c, external sac with all but a few larvae escaped through terminal aperture (op); Gng, ganglion; mn, mantle; Od, oviduct; op, external opening of brood cavity; Ov, ovary; r, nutritive roots; Tes, testis.

The parasitization of the crab by *Sacculina* adversely affects the gonads and results in structural changes of the host called *parasitic castration*. At the moult accompanying the emergence of the parasite, the male crab takes on certain female characters and the female suffers

a change from normal. Inasmuch as *Sacculina* produces only one reproductive body, the parasite has no concern with what happens to the host.

Peltogaster socialis, another rhizocephalan, differs from species of *Sacculina* in that a number of parasites, 2 to 30 of them, all in about the same stage of development, are found on the outside of one host. In his investigation of this species, G. Smith (1906) reported that each external parasite appeared to have its individual root system in the crab. Potts (1915) questioned the accuracy of Smith's observation, and suggested that more probably the several external parasites arise from a common root system, pointing out that *Peltogaster socialis* is a comparatively rare species and that it would seem unlikely that so many cypris larvae should attack the same crab at the same time.

That many external reproductive sacs may arise from one internal system of roots has been amply demonstrated by Potts (1915) in his study of the genus *Thompsonia*. Species of this genus, parasitic on various crabs, reach the ultimate in the conversion of an adult crustacean to the status of a fungus. The parasite within the host has the form of an extensive and intricate network of fine branching and anastomosing threads distributed principally on the ventral wall of the abdomen at both sides of the nerve cord, but also entering the thorax where the branches may extend up on the lateral and dorsal walls. The root threads, according to Potts, are from 10 to 20 microns in thickness. From the central network branches penetrate into the thoracic and abdominal appendages and into the lobes of the tail fan.

On the branches in the appendages are developed small budlike processes (fig. 17 E, *a*) that project outward against the integument. These buds contain the germ cells that will become ova. At the next moult of the crab they break through the soft new cuticle and become small external sacs (E, *b*, and F) standing on the surface. The sacs may be so numerous that the appendages, especially the legs, are loaded with them (fig. 15 B). These external sacs are the reproductive organs of the parasite, and might be likened to the spore-bearing bodies of a fungus mycelium. Since *Thompsonia* produces no male elements, the eggs are apparently parthenogenetic. They hatch directly into young cypris larvae (fig. 17 E), which, before the next moult of the crab, escape from the sac through an apical perforation (*op*). The empty sacs are carried off on the exuviae at the following moult of the crab. The development of the eggs, therefore, is so regulated that the larvae reach maturity during the time between moults of the host. At each moult a new crop of egg sacs breaks out on the

surface. *Thompsonia*, unlike *Sacculina*, appears to do no specific damage to its host, so that it can continue its parasitic life and indefinitely repeat its reproductive processes. The inoculation of the host by the free-swimming cypris has not been observed.

The *Thompsonia*-infested crab presents one of the most curious anomalies in the whole realm of nature. Here are two crustaceans, one inside the other, the crab a highly developed arthropod, the parasite, a crustacean relative of the crab, spread out inside the latter in the form of a network of filaments. Both host and parasite are adult animals, each being the reproductive stage of its species. Progressive and regressive evolution could hardly reach a greater degree of divergence.

Thompsonia is known to be a crustacean because it produces free-swimming cypris larvae, it is known to be a rhizocephalan because of its likeness to *Sacculina*, and *Sacculina* is known to be a cirriped because of the character of its nauplius. The barnacles and the rhizocephalans have in common the habit of attaching themselves to a support by the antennules in the cypris stage. From this point on they widely diverge. It would be highly interesting to know how the *Sacculina* larva learned to attach itself at the base of a hair on a crab, how it acquired the urge to get into the crab, and how it ever developed a self-reducing method for doing it. Halfway measures would be useless. Clearly there are problems in evolution for which natural selection does not offer a ready solution.

ISOPODA

Most of the Malacostraca are too large to be parasites. The majority are predatory, and few of them exhibit any considerable degree of metamorphosis. Most of them, moreover, hatch at a later period of development than do the Entomostraca, and some of them are almost completely epimorphic. A prominent exception to the general free mode of life, however, occurs among the isopods, a few species of which have adopted parasitism, and have become structurally adapted to a parasitic life in a degree equal to that of some of the entomostracans. This fact shows how readily metamorphosis can crop out independently in species that have adopted a new way of living.

The isopods in general are a conservative group in which the young hatch at a late stage of development with complete body segmentation and most of the appendages present. Among those that have become parasitic, however, varying degrees of adaptive metamorphosis occur

in the life history. Species that feed temporarily on the host only during the larval stages may undergo but little structural adaptation. On the other hand, species that are permanently parasitic are likely to go through a high degree of metamorphosis both in the larval and the adult stages. The two species described in the following pages, one belonging to the Gnathiidea, the other to the Epicaridea, may be taken to illustrate the two extremes of parasitic metamorphosis found among the isopods.

Paragnathia formica (Hesse).—This isopod, parasitic in its larval stage on fishes, gives us a good example of a parasite that undergoes but a minimum of metamorphic adaptation to life on its host. The developmental life history of *Paragnathia formica* has been amply described by Monod (1926) and the following account with accompanying illustrations (fig. 18) is taken from Monod's work.

The adult males and females live together in small burrows excavated in semihard mud banks of stillwater estuaries below the mean level of the ocean. Here the pregnant females in late summer or early fall give birth to active larvae. The newborn larvae leave the burrow, swimming with great speed by movements of the abdomen. Once in the open water they lose no time in attaching themselves to a fish; most any fish will do. The time between birth and attachment is a period of dispersal, during which the larva takes no food, subsisting on the remains of yolk in its alimentary canal. The larva attaches itself on the fish with its second maxillipeds, and the attack is made at any place that will readily yield blood, such as the membrane between the rays of a fin, the gills, or the mouth.

The swimming larva (fig. 18A) is a fully segmented young isopod with large compound eyes and a complete equipment of appendages. In its embryonic development it has been provided in advance with efficient piercing mouth parts and a sucking apparatus. The mouth parts (G) are enclosed in a large conical proboscis projecting forward from the head, formed of the epistome (*Epst*) above and the first maxillipeds (*1Mxpd*) below. The long, strongly toothed mandibles (*Md*) are but little movable; they serve as harpoons to hold the parasite close to the fish while the sharp-pointed, freely movable first maxillae (*1Mx*), supported by the paragnaths (*Pgn*) beneath them, puncture the integument. The much reduced second maxillae (*2Mx*) have no recognized function in feeding.

When the young larva (fig. 18A) has once established itself on a fish and has begun to feed on the blood of the host, its form changes; the change is said by Monod to be effected without the intervention of a moult. The thorax lengthens, accompanied by a swelling of the

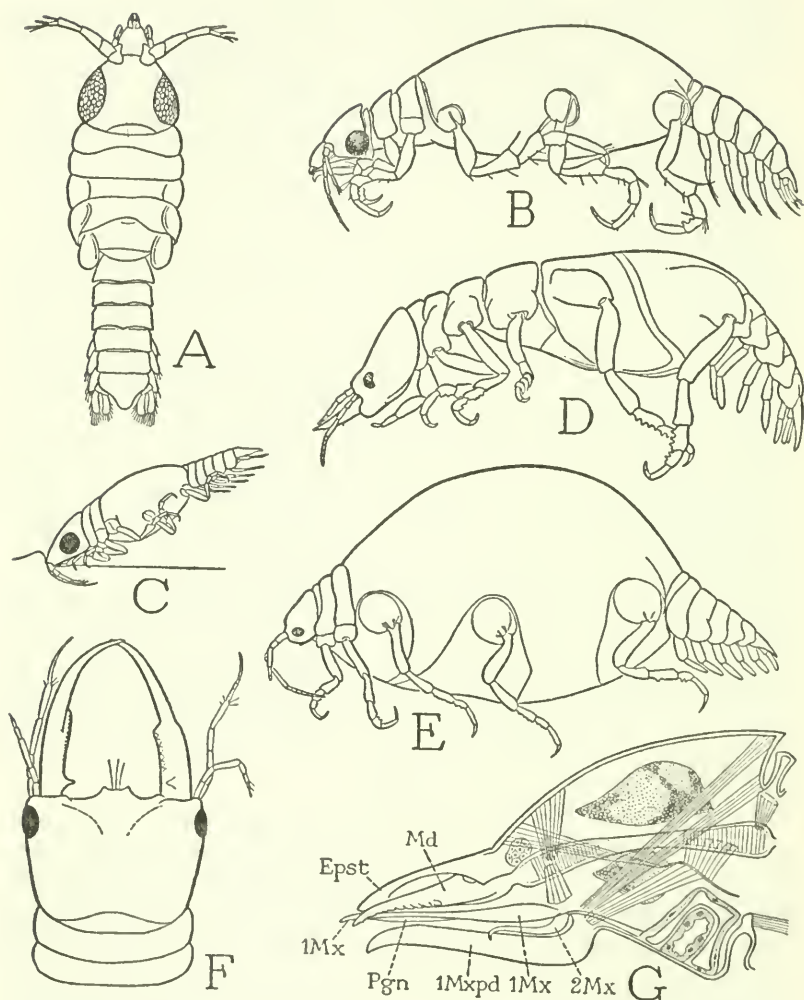


FIG. 18.—Isopoda: Gnathiidea. *Paragnatha formica* (Hesse) (from Monod, 1926).

A, first free-swimming larva. B, second form of larva parasitic on a fish. C, attitude of feeding larva. D, adult male. E, adult female. F, head of adult male, dorsal. G, section of larval head showing piercing mouth parts.

Epst, epistome; *Md*, mandible; *1Mx*, first maxilla; *2Mx*, second maxilla; *Mxpd*, maxilliped; *Pgn*, paragnath.

last three segments (B) ; the segmental limits disappear owing to the unfolding of the previously deeply infolded intersegmental membranes. This is the feeding stage of the parasite (B, C), called the *pranize* by Monod (L., prandium, lunch). Its meal lasts about six months.

At the end of winter or the beginning of spring the fully fed parasites leave the host and return to the bank of the estuary. The males individually dig burrows or take possession of empty ones in advance of the coming of the females. The completed burrows are 1.5 to 2.5 cm. in depth, sloping downward from the mouth to an inner chamber 4 or 5 mm. in diameter. When the females arrive they enter burrows already inhabited by a male; as many as 10 or more may consort with a single male. Within the burrows both the male and the females undergo their first and only moult, accompanied by a small degree of metamorphosis. The cuticle splits crosswise over the thorax, and the two ends are cast off separately. The sexes are now differentiated and the isopods enter their third functional stage, which is that of reproduction. The male (fig. 18D) retains a relatively slender figure, but the female (E) becomes greatly distended with the development of the ovaries. The mouth parts of both sexes are reduced, except the mandibles of the male (F), which are long prongs perhaps used for digging or for holding the female in mating. Subsistence is now at the expense of the food consumed during the parasitic stage.

The eggs develop into mature larvae within the ovaries of the female, which become distended into a pair of large, saclike uteri, compressing the empty alimentary canal between them. On the ventral surface of the female's thorax are several pairs of small overlapping oostegite plates, and above them is a large atrial cavity, into which the oviducts open, but this cavity does not serve as a brood chamber. When the young issue from the uteri through the oviducts into the atrium, the oostegites open and the larvae precipitate themselves head first through the aperture directly into the water, where they at once begin active swimming. After giving birth to the young, the females quickly die, but the males are longer lived and their metamorphosis is not so closely correlated with the season.

There is clearly in the life history of *Paragnathia formica* little that can be called a true metamorphosis. The change of form between the two larval phases is merely a distention and elongation of the thorax resulting from the unfolding of the intersegmental membranes. The metamorphosis at the moult to the adult stage involves principally a reduction of the mouth parts which are no longer used for feeding.

Since most isopods have biting and chewing mouth parts, the conversion of the mouth parts in the embryo of *Paragnathia* into piercing organs may be regarded as an embryonic metamorphosis preparing the future larva for its prospective life as a parasite.

Danalia curvata Fraisse.—This isopod belongs to the suborder Epicaridea, the members of which are parasitic on other crustaceans. It gives us an example of the sex versatility of some of the epicarideans in which the animal is first a functional male and then a functional female. In its female role *Danalia curvata* attaches itself to a crab infested with a rhizocephalan and feeds either on this parasite in its external state or on its roots in the host. Here the female is inseminated by a young free-swimming male, after which the male attaches to the crab and becomes a female. In this manner, though the species is hermaphroditic, it avoids self-fertilization. The following outline of the life history of *Danalia curvata* is taken from the work of G. Smith (1906) and of Caullery (1908).

The mature female (fig. 19 H) has no likeness whatever to a crustacean; she is little more than a sac full of eggs attached to the crab by a narrow stalk inserted into the crab's body. The young on hatching leave the brood pouch of the mother and become free-swimming larvae. At this stage the larva (A) is recognizable as an immature isopod, and is called a *microniscus*. The larva is distinctly segmented, has two pairs of antennae, five pairs of thoracic appendages, and five pairs of pleopods, but eyes are absent and the mouth parts are reduced to a pair of styliform mandibles enclosed in a small buccal cone. The microniscus larva may adopt a copepod as a temporary host, as do most of its relatives. After several moults it takes on a different form (B, C) and is now termed a *cryptoniscus*, presumably because its isopod characters are less evident. The body is more elongate and eyes have been developed, the appendages are retained; the cryptoniscus is a free-swimming stage. Within its body is a pair of large hermaphroditic sex organs (B), each of which contains in its anterior end a small ovary (*Ov*) and in its posterior part a large testis (*Tes*). The testes rapidly develop and become filled with an abundance of spermatozoa. The larva is now a functional male.

The male cryptoniscus seeks out a crab parasitized by a sexually mature female of his own species (G). After accomplishing the insemination of the female the larval male attaches himself to the crab or to the *Sacculina* on the crab by the first two pairs of his chelate pereopods. Then a moult takes place, the cuticle being shed in two pieces from the opposite ends of the body, and it is then seen that the larva has undergone a radical change of structure within the

cryptoniscus cuticle. The body has become a small cylindrical sac (D) about one and a quarter millimeters in length in which all trace of segmentation has disappeared. The eyes are gone, and all the

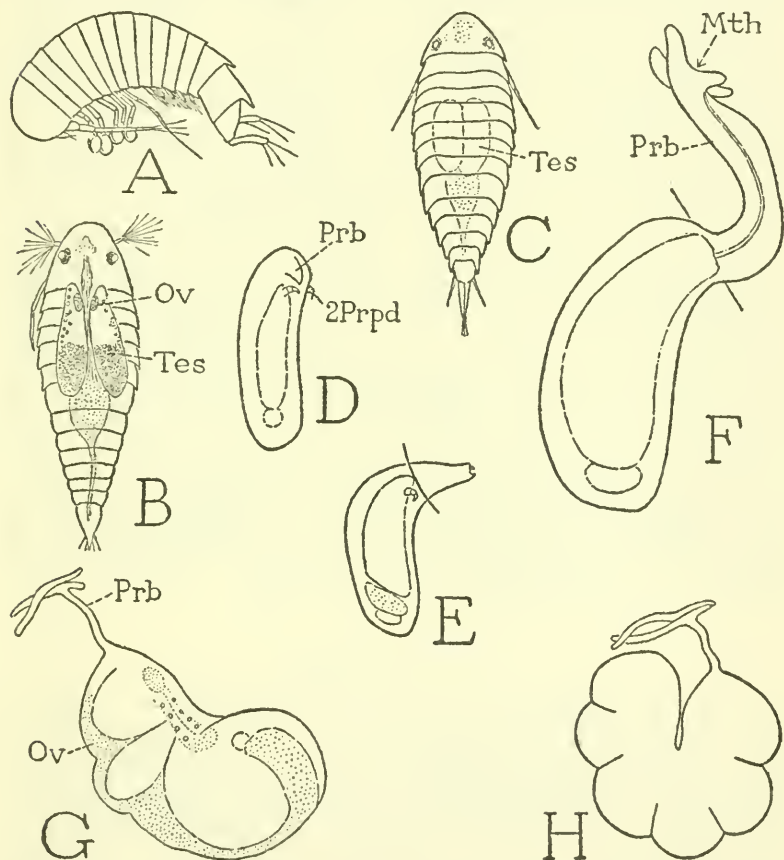


FIG. 19.—Isopoda: Epicaridea. Life history of *Danalia curvata* Fraisse. (A, C-H from Caullery, 1908; B from G. Smith, 1906.)

A, first instar larva. B, second free larval stage, with hermaphroditic sex organs containing small ovaries and large testes. C, larva with testes fully developed. D, parasitic larva on crab. E, same, with proboscis elongated. F, functional female stage, with testes degenerated, ovaries fully developed. G, female containing brood sac. H, female in final stage.

Mth, mouth; *Ov*, ovary; *Prb*, proboscis; *2Prpd*, second pereopod; *Tes*, testis.

appendages have been cast off with the exuviae except a pair of small hooklike second pereopods (*2Prpd*) with which the parasite maintains its hold on the host. A small conical proboscis (*Prb*) bears the mouth on its end. The testes, now that they have performed their

function, degenerate and the ovaries begin to develop, so that the former male larva thus changes functionally to a female.

As a female, the parasite begins to increase in size. First the proboscis elongates (fig. 19 E) and, though it is armed with only a pair of minute teeth, it penetrates the integument of the crab. Inside the host the proboscis stretches out to a long neck (F, *Prb*) until the mouth (*Mth*) at the end comes in contact with the roots of the *Sacculina*, and four diverging processes grow out around the mouth to anchor the proboscis in the tissues of the crab. The body of the newly feminized individual then takes on a saclike form (G). The ovaries (*Ov*) are now fully developed; the oviducts open on two pairs of ventral papillae. At this stage the female is inseminated by a cryptoniscus larva still in the male phase of development (C). The fertilized eggs are discharged into a large incubation chamber beneath the cuticle of the female. The process of forming the chamber is somewhat complex as described by Caullery, but essentially it appears that two lateral ingrowths of the ventral ectoderm extend inward around the sides of the body, and eventually close over the orifices of the oviducts. When the eggs are discharged into the incubation chamber, the female ceases to feed, doubles on herself in the form of a U (H) and becomes a mere inert sac in which the eggs complete their development.

EUPHAUSIACEA

The Euphausiacea and some of the Penaeidae are exceptional among the Malacostraca in that they are hatched as nauplii. They are both marine and entirely pelagic. The euphausiids go through many moults before reaching the adult stage. Students of the group commonly distinguish five immature stages in the life history of an individual. The first two are the nauplius and the metanauplius, the following three stages are termed the *calyptopis*, the *furcillia*, and the *cyrtopia*. These forms, however, are merely stages of growth characterized by different degrees of differentiation toward the adult structure (fig. 20 A-G). Except for the successive specialization of different groups of appendages for swimming there are few metamorphic changes involved in the development. The following condensed account of the typical life history of a euphausiid species is based on the papers by Heegaard (1948) and Lebour (1925), with illustrations taken from both. The order includes only a single family, the Euphausiidae.

The newly hatched euphausiid larva (fig. 20 A) is a typical nauplius of simple form with the usual three pairs of appendages, a simple

median eye, and a large labrum. The metanauplius (B) acquires three additional pairs of appendages, which are the first and second maxillae and the first pair of legs (1L), or maxillipeds. The mandibles (Md)

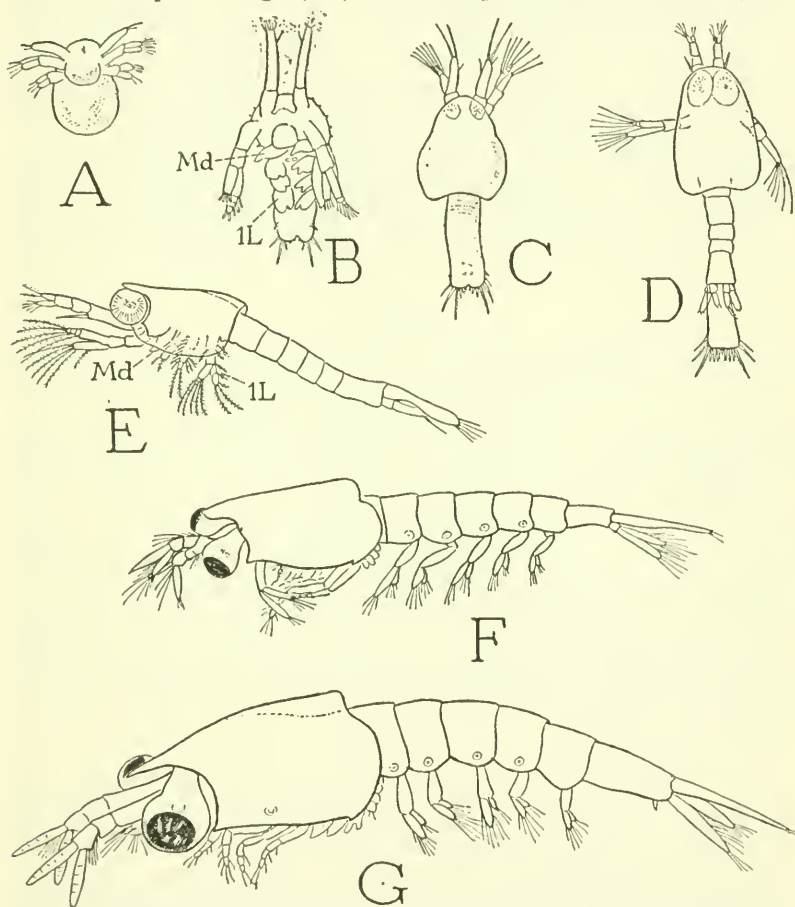


FIG. 20.—Euphausiacea. Life-history stages. (A-E from Heegaard, 1948; F, G from Lebour, 1925.)

A, *Meganyctiphanes norvegica* Sars, nauplius. B, same, metanauplius. C, same, first calyptopis instar. D, same, third calyptopis instar. E, same, first furcillia instar. F, *Nyctiphanes couchii* Bell, last (12th) furcillia instar. G, *Meganyctiphanes norvegica*, first cyrtopia instar.

have become jawlike. The metanauplius is followed by the calyptopis stage, which at an early instar (C) is characterized by the distinct development of the carapace and the elongation of the abdomen. The median eye is replaced by sessile rudiments of compound eyes concealed beneath the carapace. The appendages are those of the metanauplius. At a later calyptopis instar (D) the abdomen has become

segmented and the uropods are developed. In the furcillia stage (E, F) the larva begins to resemble the adult. The eyes are now stalked and project from beneath the carapace. The first furcillia instar (E) has still only the appendages of the metanauplius, but after the first moult the pereopods appear as simple papillae, which later enlarge (F, G) and finally become biramous appendages. At the same time the pleopods are formed. According to Lebour (1925) in *Nyctiphanes* and *MeganNyctiphanes* there are 12 furcillia instars separated by moults. In the final cyrtopia stage (G), after 8 to 13 moults according to the species, the young euphausiid acquires the adult structure with a complete set of appendages and luminescent organs.

DECAPODA

The decapod crustaceans include the shrimps, lobsters, crayfishes, and crabs. None of them exhibits any pronounced metamorphic changes during development or in the adult stage, but most of them go through stages of growth characterized chiefly by the successive development of sets of appendages. Only in the Penaeidae is there a free nauplius and a metanauplius. Most species hatch in a form called a *zoea*, in which the appendages following the second maxillipeds are as yet undeveloped or are present as rudiments. With the functional completion of the pereopods the larva is known as a *mysis* from its fancied resemblance to a member of the Mysidacea. Some species, however, go through the zoea stage in the egg and hatch as a *mysis*, and a few are almost completely developed in the adult form on leaving the egg.

The decapod larvae are free swimming, and in general are fairly uniform in structure with a fully developed carapace and a long segmented abdomen. A few, however, take on unusual forms. Among the Sergestidae many of the larvae are characterized by a great development of long, often profusely branched spines on the thorax and abdomen. The rounded carapace of the palinuran *Polycheles* larva looks like a spiny burr, and others of the same group, known as phyllosome larvae, are broad, flat, and leaflike in shape. Presumably such forms are adaptations to buoyancy or floating.

The Penaeidea.—In this order the family Penaeidae is of particular interest because it includes the only decapods that begin life as free-swimming nauplii. The fact that among the Malacostraca both the penaeids and the euphausiids hatch from the egg as nauplii may be taken as evidence that primarily all the crustaceans hatched at this early stage of development, and that later hatching among the higher Malacostraca is secondary, resulting from the earlier stages being

completed for better security in the egg. The life history of *Penaeus setiferus* (L.) is now well known from the studies of Pearson (1939) and Heegaard (1953), and will here be briefly reviewed from the papers by these two authors. The penaeid life history, moreover, will serve also as a good subject for a discussion of the significance of crustacean larval forms.

Both the nauplius and the metanauplius of *Penaeus* (fig. 21 A, B) have long swimming appendages, but the alimentary canal is not yet developed and the larvae in these stages subsist on the yolk derived from the egg. In the metanauplius (B), however, the mandibles have acquired gnathal lobes on their bases, and rudiments of four pairs of postmandibular appendages are present, the last being those of the second maxillipeds (2*Mrpd*). The metanauplius goes over into the zoeal stage, in which there are three instars. In the first zoea (C) the carapace has developed, the mandibles have become functional jaws, and the larva now takes its first external food. The following appendages have developed into biramous limbs, and the abdomen shows a faint trace of segmentation, but the larva apparently still swims by means of the antennae. In the third zoeal instar (D) the larva takes on something of the adult form (G). The carapace covers the thorax, and rudiments of the pereopods (D, *Prpds*) are present, the abdomen is fully segmented but pleopods have not yet appeared, and the antennae are still the chief organs of propulsion. The third zoea is followed by the so-called mysis stage, which goes through two instars. In the first mysis (E) the pereopods are all present and have long seta-bearing exopodites, which now assume the locomotor function, and the antennae are reduced. The abdomen has well-developed uropods, but pleopods are as yet absent.

The next stage (fig. 21 F), known as the *postmysis*, or *postlarva*, more nearly resembles the adult. The pereopods have lost their exopodites, and those of the first three pairs are chelate. Slender uniramous pleopods are present on the abdomen and are now the swimming organs as they are in the adult. In the adult (G) the pleopods have acquired the typical biramous structure, and a long filamentous flagellum arises from each second antenna.

The life-history stages of *Lucifer*, as described by Brooks (1882), are similar to those of *Penaeus*, except that the larva hatches as a metanauplius and the animal takes on a different form in its preadult and mature stages. Numerous examples of the bizarre larvae of Sergestidae, characterized by long, branched spines on the thorax and abdomen, are illustrated by Gurney (1924).

There has been much discussion among carcinologists as to whether or not the forms of decapod larvae have a phylogenetic significance.

Gurney (1942) has pointed out that "the larval stages of today provide evidence for phylogeny, but indirectly," since the ontogeny of an animal recapitulates the ontogeny of its ancestors.

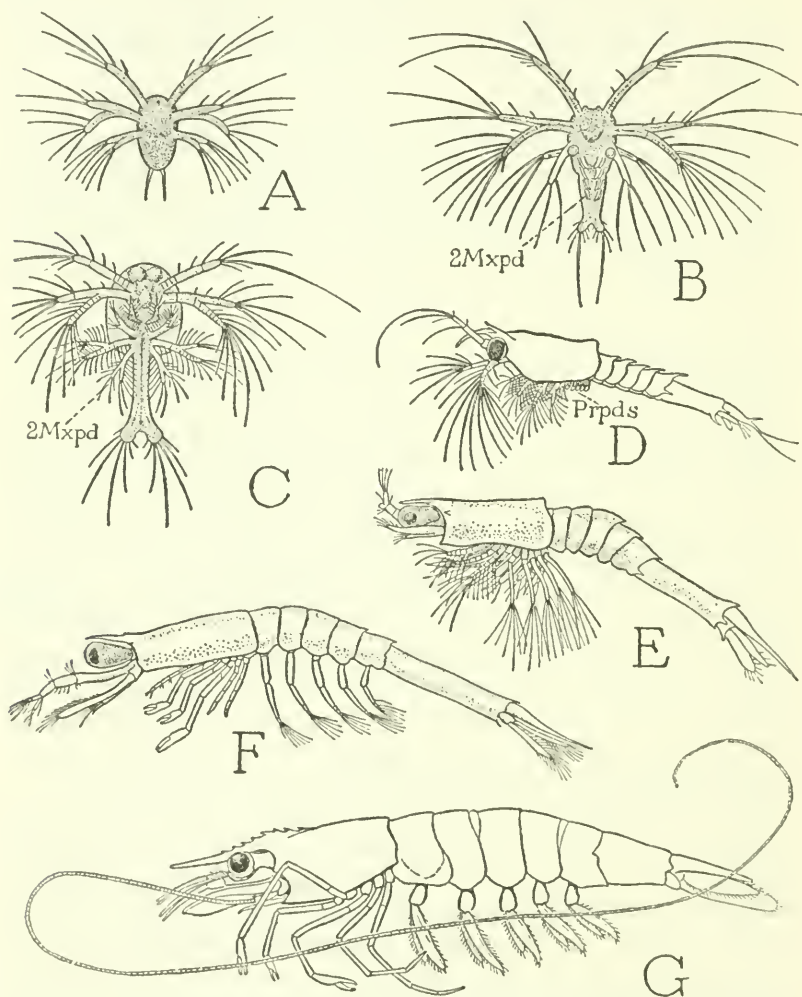


FIG. 21.—Decapoda: Penaeidea. Developmental stages of *Penaeus setiferus* (L.). (A-F from Pearson, 1939.)

A, first nauplius. B, metanauplius. C, first protozoaea. D, third protozoaea. E, first mysis. F, first postmysis. G, adult.

2Mxpd, second maxillipeds; *Prpds*, rudiments of pereopods.

It is true that ontogenetic stages of a species may represent in a modified way adult ancestral stages of phylogenetic evolution. The adult ancestry of a crustacean, however, can go back only as far as

the primitive adult arthropod from which the Crustacea were evolved. Life-history stages representing adult crustacean ancestors, therefore, can be recapitulations only of forms that intervened in evolution between the primitive arthropod and the modern crustacean.

On the assumption adopted in the early part of this paper as a basic concept, the primitive arthropod is presumed to have been an elongate, segmented animal with a pair of similar jointed appendages on each body segment (fig. 1 C). From such a progenitor all the modern arthropods were evolved by special modifications, particularly of the appendages, according to the adopted way of living. *Anaspides* (D) may be taken as an example of a fairly generalized modern crustacean, but other crustaceans go through no developmental stage resembling *Anaspides* or any other form that might be intermediate between their adult structure and that of a primitive arthropod. The megalops of a crab undoubtedly represents an early crab form, but there is little evidence that the Crustacea in general recapitulate adult stages of crustacean ancestry or the adults of other species of lower rank in taxonomy. There is no reason to believe that the likeness of the "mysis" stage of the penaeid (fig. 21 E, F) to an adult *Mysis* is anything more than a superficial resemblance. Foxon (1936) has shown that the decapod larvae do not go through a typical euphausiid or mysid stage, and that neither the structure nor the function of the mysid appendages is recapitulated in other groups. The precocious development of the uropods before the pleopods are formed is explained by Foxon (1934) as an adaptation to reverse movement.

Most crustaceans develop by anamorphosis, but the anamorphic method of growth was established in the remote progenitors of the arthropods before the arthropods became arthropods. The embryo in the egg goes through the preanamorphic stages of its ancestors, and if it is hatched as a nauplius, the following ontogenetic stages recapitulate the anamorphic steps of precrustacean evolution. The larva, however, is destined to be a crustacean, it carries the genes of its species, and its crustacean destiny is thus stamped on it before it leaves the egg. Hence, from the beginning of its development the larva takes on crustacean characters, but the forms it assumes are ontogenetic and not recapitulations of adult crustacean evolution. When the larva is set free at a very immature stage it must be structurally adapted to the exigencies of an independent life, and it may be modified for a way of living that was not at all that of its ancestors. Thus the normal ontogenetic stages may take on metamorphic aberrations having no relation to anything in the past history of the animal

or to its own future adult stage. Such nonancestral forms are particularly evident in parasitic species.

Gurney (1942), referring to the progressive shift of the swimming function in the larva from the antennae to the pereopods and finally to the pleopods, has expressed the idea that "the fundamental fact which determines the organization of the larva is the mode of locomotion." However, it is to be presumed that the use of the pleopods for swimming was first established in the adult ancestors of such species. The nauplius naturally cannot swim in this ancestral manner, and must use what appendages it has. As the larva grows by the addition of segments and appendages it can more efficiently swim by making use of the pereopods, and finally when the pleopods are developed it can swim in the adult manner. It is the progressive organization of the larva, therefore, that determines the mode of locomotion.

The Macrura.—The macruran decapods are the lobsters and the crayfishes. The lobster, *Homarus*, according to S. I. Smith (1871-1873) undergoes its early development in the egg and hatches at a stage when all the pereopods are present and are equipped with feathery exopodites. This first free stage of the lobster (fig. 22 A), therefore, corresponds with the mysis stage of *Penaeus* (fig. 21 E). In the next instar the larva increases somewhat in size, and rudiments of pleopods appear on the abdomen. In the third instar (fig. 22 B) the young lobster attains a length of 12 to 13 mm. and much resembles the adult; the chelae are well developed, the pleopods are biramous, but the exopodites are still present on the pereopods. Smith suggests that there is probably another instar intervening between the third and the adult when the exopodites are lost, as in the postmysis of *Penaeus* (fig. 21 F).

The fresh-water crayfishes, *Astacus* and *Cambarus*, hatch at a later stage of development than *Homarus*, when they have practically the adult structure except for the lack of the first and sixth pleopods.

The Brachyura.—The brachyurans, or "short-tailed" decapods, are the ordinary crabs, so named because of the small size of the abdomen, which in the adult is carried bent forward beneath the thorax. The zoal larvae are characterized in most species (fig. 23) by the presence of a long dorsal spine on the thorax and by the spinelike form of the rostrum, the two often projecting in a straight median line from opposite ends of the back. Some have also lateral spines. The larva swims with the large first and second maxillipeds, and the spines are supposed to assist in directing the course of the larva in the water or to help keep it afloat. The spines are absent in only a few species, as in the genus *Ebalia* and in members of the Pinnotheridae. The last

zoea transforms into a preliminary crablike stage known as a *megalops*.

The life history of the blue crab of the Chesapeake Bay, *Callinectes sapidus* Rathbun, has been studied by Churchill (1942), Hopkins (1944), and Sandoz and Hopkins (1944), and is typical of the development of most of the Brachyura. The young crab is sometimes hatched in a final embryonic stage called by Churchill a *prezoea* (fig. 23 A). It is still enclosed in a thin, transparent, closely fitting cuticle

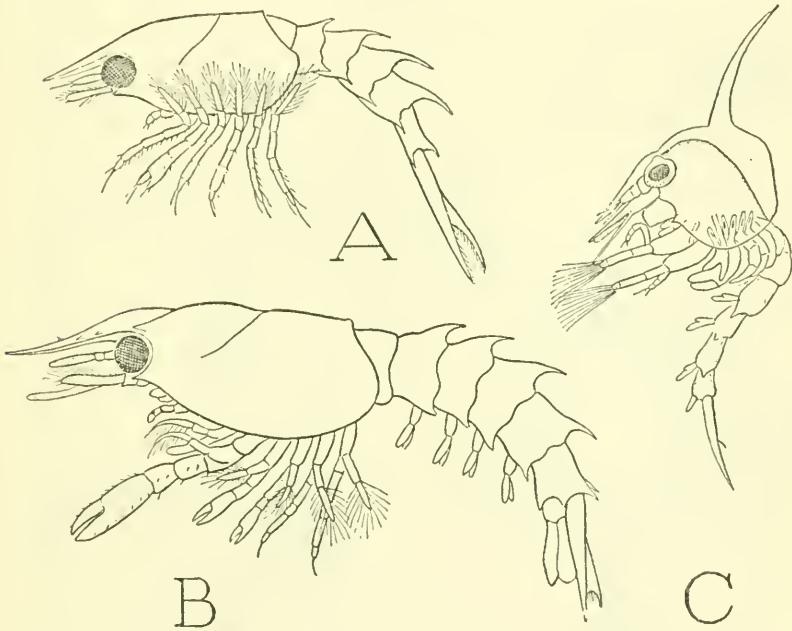


FIG. 22.—Decapoda: Macrura and Brachyura. Young stages. (A, B from S. I. Smith, 1871-1873; C from Cano, 1891.)

A, *Homarus americanus* H. Milne Edw., first larval instar, zoea. B, same, third instar. C, *Pilumnus*, a brachyuran crab, metazoea with partly developed chelipeds and pereopods.

that covers the spines, which will be exposed at the first moult. Sandoz and Hopkins say that emergence in the prezoeal stage results from unfavorable conditions at the time of hatching. The first free larva is a typical crab zoea (B) about 0.85 mm. in length. It has a short, rounded carapace and a long, slender, segmented abdomen. The last appendages are the large first and second maxillipeds, the exopodites of which are equipped with terminal fans of long featherlike bristles. The sixth segment of the abdomen is still united with the telson. In the second zoea (C) there is no essential change of structure, but the

body and appendages have increased in size. Churchill describes five zoeal instars in *Callinectes sapidus*, but his figures of the third, fourth, and probably the fifth instar are said by Hopkins (1944) to be larvae of some other crab. The differences, however, are slight and pertain mostly to the number of setae on the appendages and spines on the abdomen. In the fifth instar (D) the last abdominal segment is separated from the telson and pleopods are present. About the only

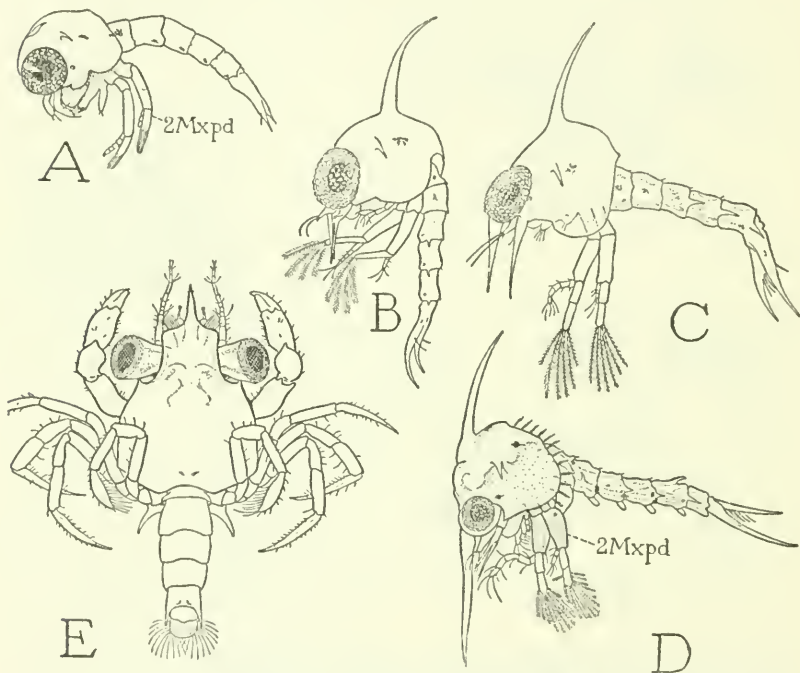


FIG. 23.—Decapoda: Brachyura. Larval stages of *Callinectes sapidus* Rathbun (from Churchill, 1942).

A, prezoa. B, first zoea. C, second zoea. D, fifth zoea. E, megalops.

metamorphic features of the crab zoea are the development of the dorsal and rostral spines and the adaptation of the maxillipeds for swimming.

During the zoeal stage buds of the third maxillipeds and of the pereopods appear on the thorax beneath the carapace and increase in length in successive instars, but they are not seen in Churchill's figures (fig. 23). It seems hardly likely that the zoea shown at D of the figure could go over directly into the megalops (E). In the final zoea of other crabs, sometimes called a *metazoea*, the appendages behind the second maxillipeds are well developed, as shown by Cano

(1891) in the metazoea of *Pilumnus* (fig. 22 C). The first and second maxillipeds still have the zoeal structure, but they are followed by the third maxillipeds and five pairs of pereopods, of which the first are strongly chelate. Moreover, all these newly developed appendages except those of the last two pairs support branchial lobes on their bases. Similar advanced larval instars are shown for several other species of Brachyura by Lebour (1928). Hence, we should assume that there must be in *Callinectes* a metazoeal instar in which the thoracic appendages are in a state of development that could go over at one moult into the appendages of the megalops. In the life history of the crab there is no form corresponding to the mysis stage of *Penaeus* (fig. 21 E) or that of *Homarus* (fig. 22 A), but the metazoea might be likened to the postmysis of *Penaeus*.

The megalops (fig. 23 E) is clearly a young crab, though it is only a few millimeters in length. The dorsal spine of the zoea has been shed with the larval cuticle (fig. 22 C) and the rostrum is shortened to the ordinary length. The swimming maxillipeds are transformed into feeding organs, and the other appendages are those of the adult. The prominent stalked eyes give the megalops its name ("bigeye"). An important feature of the megalops, however, is the extension of the abdomen from the thorax, which suggests that the megalops represents an adult ancestral form of the crab before the latter permanently flexed its abdomen forward beneath the thorax.

The adult crab on issuing from the cuticle of the megalops is still a minute creature and goes through a large number of instars before becoming sexually mature, after which it may continue to moult at intervals. The habits of adult crabs are more various than those of the larvae. While most adult crabs live in the ocean and crawl on the bottom, some of them live in the shells of mollusks, in echinoderms, in cavities of corals, and in tubes of worms. Others have left the water for the land, where they dig deep burrows in the sand above high water, and still others go freely inland, even invading human habitations. The famous anomuran robber crab of the South Sea Islands is said to climb cocoanut trees for their nuts. Regardless of their habits or the nature of their dwellings, however, the brachyuran crabs have undergone little structural adaptation. They vary in size and shape, in the relative size of the chelae, and in the length of their legs, but in general they retain the typical crab structure. Among the Anomura, however, a pronounced adaptive modification of the body occurs in the hermit crabs that live in snail shells. The carapace of these crabs is weak and flexible. The abdomen is a long, soft sac that

fills the cavity of the snail shell; pleopods are present generally on the left side only, but the uropods are strong, recurved appendages evidently serving to secure the crab in its house.

STOMATOPODA

The stomatopods are an individualistic group of malacostracans having some relatively primitive features in combination with so many structural specializations that it is difficult to give them a definite place in taxonomy. The head of the adult animal (fig. 24 G), projecting from beneath a small rostral lobe of the carapace, has a complex structure not found in any other crustacean. The short, narrow carapace covers only the gnathal region and the first four thoracic segments. The other four free segments of the thorax are symmetrical with the large abdomen, and appear to be a part of it except for the leglike appendages borne on the last three. The limbs of the first, third, fourth, and fifth thoracic segments are turned forward and each bears a small apical chela; but those of the second segment ($2L$) are huge raptorial organs in which the terminal segments are long, strongly toothed claws, each closing tightly against the penultimate segment, giving the stomatopod its likeness to the insect praying mantis (which is not responsible for its name). The large abdomen has five pairs of pleopods, and the stomatopod gills are borne on the pleopods. The uropods are large, biramous appendages; the telson is a broad spiny plate.

The adult stomatopods are mostly littoral in their habits. Though they swim freely, they live principally in burrows in the sand or mud of the bottom. The females lay their eggs in a mass beneath the fore part of the body, where they are held between the raptorial legs by the four small chelate legs of the thorax. The eggs are carried in this manner until the young larvae emerge, a period said by Giesbrecht (1910) to last for 10 or 11 weeks.

The young stomatopods are hatched in two different larval forms, which seem to have no developmental relation to each other. Our best source of information on the larval stages will be Giesbrecht's (1910) elaborate monograph on Mediterranean species. Gurney (1946) gives descriptions and good illustrations of various stomatopod larvae, but no full account of the life history of any one species. Alikunhi (1952) describes and figures particularly the last-stage larvae of Indian species.

The simpler first-stage larval form pertains to species of *Lysiosquilla* and *Coromida*, and is termed by Giesbrecht an *antexoea*. This

larva (fig. 24 A) is from 2 to 2.25 mm. in length. The thorax is fully segmented and is entirely covered by the carapace. The abdomen (*Ab*) is either unsegmented and entirely united with the telson (*Tel*)

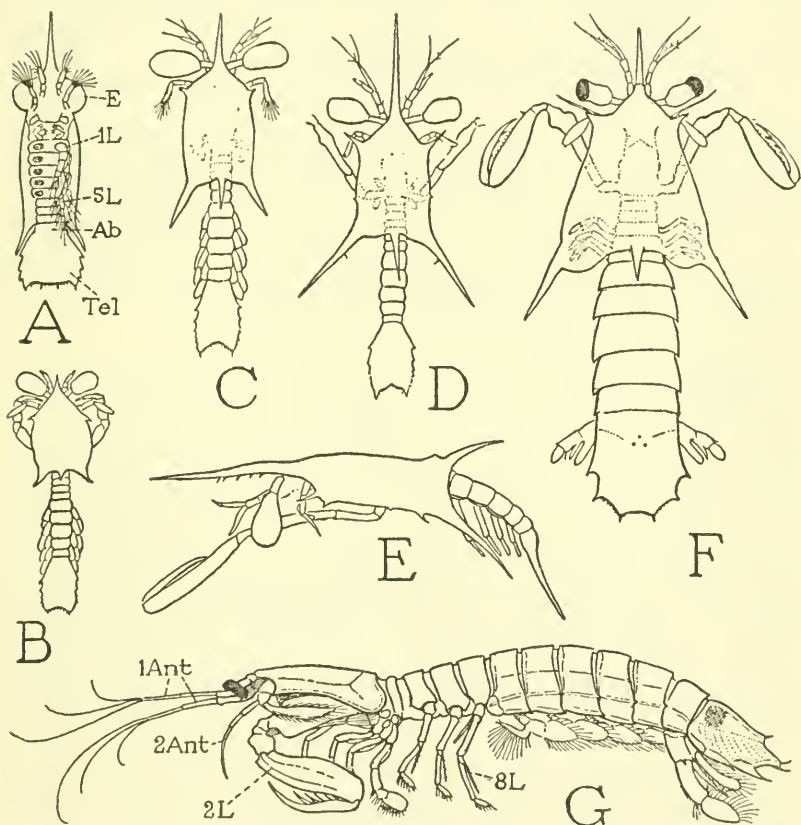


FIG. 24.—Stomatopoda. Larval stages and an adult. (A-E from Giesbrecht, 1910; F from Alikunhi, 1952.)

A, an antezoea larva. B, *Squilla mantis* Latr., first propelagic stage. C, same, second propelagic stage. D, same, first pelagic stage, dorsal. E, same, first pelagic stage, lateral. F, *Squilla latreillei*, last pelagic larval stage. G, *Squilla mantis*, adult male.

Ab, abdomen; *1Ant*, first antenna; *2Ant*, second antenna; *E*, eye; *1L*, *2L*, *5L*, *8L*, first, second, fifth, and eighth thoracic appendages; *Tel*, telson.

in a wide, fan-shaped plate, or one or two anterior segments may be free. The eyes (*E*) are large but sessile. The first five thoracic segments bear each a pair of small, biramous appendages (*1L*, *5L*) used for swimming. The antezoeal larva is pelagic. During subsequent

stages of its growth, the abdominal segments are successively separated from the telson and acquire pleopods. The five thoracic appendages lose their exopodites and take on the adult form, those of the second segment becoming typical raptorial fangs in the fourth instar. Later the appendages appear on the last three segments of the thorax. In the second instar the eyes are stalked.

The other first-larval form, termed a *pseudozoea* (fig. 24 B), occurs in species of *Squilla*, *Gonodactylus*, and probably of other genera. The eyes in this form are stalked at hatching. The thorax is fully segmented, but only the first two segments bear appendages, and those of the second segment are raptorial fangs. The short carapace has small spines on its anterior and posterior angles, and leaves four posterior thoracic segments uncovered. The abdomen has five free segments, of which the first four bear pleopods, but the sixth is still united with the telson.

Squilla mantis, according to Giesbrecht, goes through 10 larval instars. The first two live on the bottom, but after the second instar the larva becomes pelagic, swimming with the pleopods. In the second propelagic instar (fig. 24 C) there is little change from the first (B) except for an increase in size and a lengthening of the posterior carapace spines, which in the first pelagic instar (D, E) become much longer and widely divergent. In the third pelagic instar rudiments of the third, fourth, and fifth thoracic appendages appear, and become longer in the next stage, when also the appendages of segments six, seven, and eight are developed. The sixth segment of the abdomen becomes free from the telson in the seventh instar. The last pelagic larva (F) has essentially the structure of the adult (G) except for the large carapace, which now covers all but one of the thoracic segments. After about the fifth instar, Giesbrecht says, the two larval forms, originating with the antezoea and the pseudozoea, become structurally alike.

The principal structural changes during the life of the stomatopod take place at the transformation of the larva (fig. 24 F) into the adult (G). Even here, however, the only essential change affects the carapace, which is much shortened and narrowed and loses its posterior spines. Instead of covering most of the thorax as in the larva (D, F) the carapace of the adult leaves the last four thoracic segments exposed. In this respect the carapace reverts to its relative length in the first propelagic larva (B). It is evident, therefore, that the larval development of the back shield is a metamorphic adaptation to the pelagic life of the larva, probably to assist in keeping the larva afloat. The relative length of the larval carapace varies in different

species. In some forms the last four thoracic segments are not covered, as in the adult of *Squilla* (G), in others such as *Squilla latreillei* (F) only the eighth segment is exposed in the larva, while in species of *Lysiosquilla* the carapace of the last larva may cover the entire thorax and the first two abdominal segments. Probably these variations in the length of the larval carapace are only differences in the extent to which the free posterior margin is produced beyond the attachment of the plate on the third or fourth segment of the adult thorax. Otherwise the changes during the growth of the larva are merely developmental stages of growth and have no metamorphic value. It is difficult even to see any functional reason for the differences between the two larval forms on hatching.

IV. STRUCTURE AND EVOLUTION OF ARTHROPOD APPENDAGES

Inasmuch as changes in the form and function of the appendages are important features in the metamorphoses of Crustacea, and various conflicting views have been held concerning the primitive nature and the evolution of arthropod limbs, we must give some attention to this controversial subject.

Most studies on the comparative structure of the arthropod appendages, and deductions as to the origin and primitive form of the limbs give the impression that conclusions have resulted too much from an attempt to fit the facts into a preconceived theory. Widely accepted has been the idea that the primitive appendage was a biramous limb; and many carcinologists would derive all kinds of arthropod appendages from an original phyllopodial type of limb, such as that of the branchiopod crustaceans.

The trilobites are among the oldest known arthropods, and, with respect to their appendages, they are the most generalized, since all the postoral limbs are fully segmented legs. The base of each leg bears a branched lateral process (fig. 25 A, *Eppd*), which, arising on the coxa, is clearly an epipodite and hence cannot be an equivalent of the crustacean exopodite, which by definition is an exite of the basipodite. The trilobite limb, therefore, is not "biramous" in the manner of a crustacean limb, and hence does not relate the trilobites to the Crustacea. Raymond (1920), however, explicitly states the opposite view. "The trilobites," he says, "are themselves crustaceans, as is amply proven by their biramous appendages." More recently, Heegaard (1947) has argued that the trilobite limb is truly biramous, in spite of the evident coxal position of the "exopodite," and he further attempts to show that remnants of a primitive biramous structure are

to be found in various modern arthropods other than the Crustacea. His discussion, however, takes too many liberties with simple visible facts in an endeavor to fit them into a consistent scheme of structure. The studies of trilobite appendages by Störmer (1939) leave little doubt that the trilobite leg (fig. 25 A) is simply a uniramous, segmented limb with a coxal epipodite that was perhaps a gill. Störmer's contention, however, that a narrow ring at the base of the coxa is a

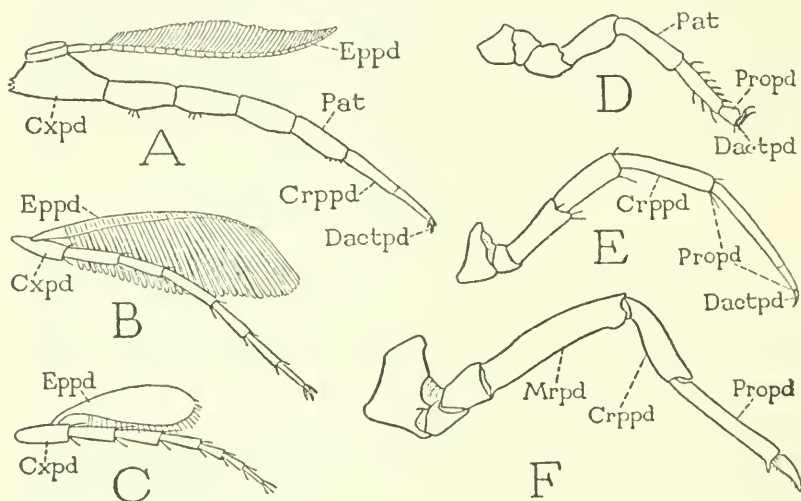


FIG. 25.—Examples of segmentation of arthropod legs.

A, leg of a trilobite (from Störmer, 1939). B, leg of *Marella* (adapted from Walcott, 1931). C, leg of *Burgessia* (from Walcott, 1931). D, leg of solpugid arachnid. E, leg of a chilopod, *Lithobius*. F, leg of a decapod, *Cambarus*.

Crppd, carpopodite (tibia); *Cxpd*, coxopodite (coxa); *Dactpd*, dactylopodite (pretarsus); *Eppd*, epipodite; *Mrpd*, meropodite (femur); *Pat*, patella; *Propd*, propodite (tarsus).

precoxal segment is questionable. The coxa of other arthropods is often marked by a circular groove near the base that forms an internal strengthening ridge giving attachment to the body muscles of the limb. In the trilobite leg the large coxopodite should be the movable basal segment of the limb and not the narrow "precoxa."

The idea that the primitive arthropod limb was a flat, lobulated appendage of the phyllopodial type has been accepted by some carcinologists regardless of the fact that the limbs of the trilobites (fig. 25 A) and of associated fossil forms such as *Marella* (B) and *Burgessia* (C) are slender jointed legs, as are those of nearly all modern arthropods (D, E, F), including the Malacostraca (F).

Walcott (1931), for example, in discussing his Burgess Shale fossils seems to accept this theory without question when he says: "The biramous limb of *Marella*, like that of the trilobite, undoubtedly passed through the foliaceous or multiramous limb stage in its evolution, probably in pre-Cambrian time." There is no disproving this idea, which should apply to the other arthropods as well, but such implicit faith in a theory is hard to understand.

On the other hand, Raymond (1920) says the theory of the phyllopod origin of the arthropod limb "has been completely upset" by the finding of such "undoubted branchiopods" as *Burgessia* in the Middle Cambrian with trilobitelike legs. The same idea has been expressed by Heegaard (1947) in his statement that the "undoubted branchiopods" found by Walcott in the Middle Cambrian having trilobite legs show that "it can no longer be held that the phyllopodial limbs are primitive." The writer fully agrees with this conclusion, but for different reasons than those given by Raymond and Heegaard. Such fossils as *Burgessia* and *Marella* are certainly not "undoubted" branchiopods. Walcott (1931) says of *Marella* that it is a less primitive form than the Apodidae and more primitive than the trilobites, but is nearer to the latter than to the former. Among the Middle Cambrian fossils, however, is a form, *Opabina regalis* Walcott, particularly studied by Hutchinson (1930), which evidently is an anostracan branchiopod with foliaceous appendages.

Another popular belief concerning the derivation of the arthropod limb, taken to support the theory of its biramous phyllopodial origin, is that the limb was evolved from the polychaete parapodium. Reasons have already been given in section I of this paper for believing that the annelids have only a remote connection with the arthropod progenitors. Certainly the arthropods can have no relation to modern polychaetes, which are highly specialized annelids and could give rise only to more polychaetes. The appendages of the worm, though they are bilobed flaps, have a lateral position on the body (fig. 26 A), and there is nothing in their structure having any likeness to an arthropod limb at any stage of its development. The parapodium bears two bundles of bristles supported on a pair of long internal rods giving attachment to muscles. Its only common feature with an arthropod limb is that, being a locomotor organ, it is movable forward and backward by body muscles. In short, the idea that the arthropod appendages were derived from annelid parapodia appears to be just another case of excessive zeal for generalization.

Among modern wormlike animals those closest to the arthropods are the Onychophora; some zoologists have even included the ony-

chophorans in the Arthropoda. Though a modern onychophoran shows no external segmentation of the body in the adult stage, the segmented repetition of internal organs and the complete body segmentation of the embryo leave no doubt that the Onychophora are

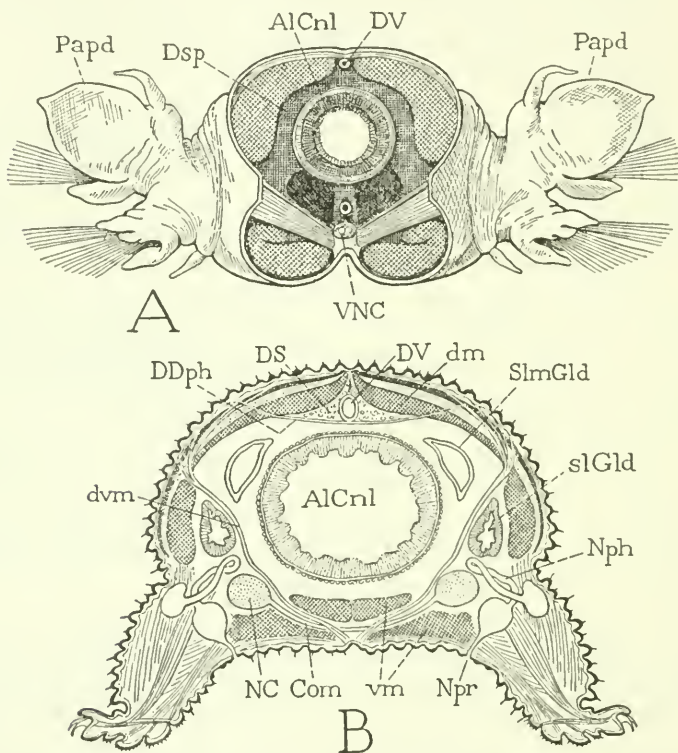


FIG. 26.—Diagrammatic transverse sections of *Nereus* (A) and *Peripatus* (B), showing comparative structure of the appendages of a polychaete annelid and an onychophoran.

AlCnl, alimentary canal; *Com*, nerve commissure; *DDph*, dorsal diaphragm; *dm*, dorsal muscles; *DS*, dorsal sinus; *Dsp*, dissepiment; *DV*, dorsal blood vessel; *dvm*, dorsoventral muscles; *NC*, lateral nerve cord; *Nph*, nephridium; *Npr*, nephropore; *Papd*, parapodium; *SlmGld*, slime gland; *vm*, ventral muscles; *VNC*, ventral nerve cord.

fundamentally metameric animals. The body cavity is undivided by dessepiments, the primitive coelom is represented only by the lumina of the nephridia and the gonads, and the embryogeny of the Onychophora gives the key to the early embryonic development of the arthropods. The onychophoran legs have a lateroventral position on the body (fig. 26 B) as in the arthropods, in contrast to the lateral posi-

tion of the polychaete parapodia (A). The nephridia (B, *Nph*) and the primitive genital ducts open mesad of the leg bases suggestive of their openings on the coxae in many of the arthropods. Though modern Onychophora are terrestrial animals, there can be little doubt that they had aquatic ancestral relatives represented by the Cambrian *Aysheaia* of the Burgess Shale, and perhaps by the Pre-Cambrian *Xenusion* described by Heymons (1928).

The arthropod limbs are developed on the embryo from latero-ventral budlike rudiments that lengthen and become segmented. We may therefore suppose that from the ancestral onychophorans (fig. 1 A) a form was evolved with longer legs (B), which later, with sclerotization of the integument, became the jointed appendages of the ancestral arthropods (C). It then required a long period of Pre-Cambrian evolution to produce a trilobite on the one hand, and some ancestral form of crustacean on the other. The differentiation between the two groups, however, was first in the form of the body, not in that of the appendages, as seen in the legs of a trilobite (fig. 25 A) and those of *Marella* and *Burgessia* (B, C). Though there is no valid reason for regarding the primitive arthropod appendage as being a biramous limb, the crustacean appendages later acquired their characteristic biramous structure, which is usually lost in the ambulatory limbs (F).

Many carcinologists hold the view that the phyllopodial type of limb is primitive, at least for the Crustacea, and this concept has been well elucidated by Borradaile (1926a, 1926b). It is supposed that the primitive crustacean appendage was a flat, unsclerotized lobe with a fringe of hairs on the mesal border. Then the inner margin was broken up by the development of a series of endites. Next, the limb became more rigid by a sclerotization of the integument, but this necessitated lines of flexibility that led to a system of jointing, and naturally the joints were formed between the endites. Thus the endites are explained as the precursors of the later developed limb segments. Finally, with the departure from the phyllopodial form and the suppression of the endites, some of the limbs became slender, segmented, leglike appendages. In favor of this theory it may be noted that in many of the branchiopod appendages there are six endites on the mesal margin and a free lobe at the apex (fig. 27 A, B). If all the parts of such a limb became segments there would be seven segments in all, the terminal lobe becoming the dactylopodite, which gives the usual number of limb segments in the Crustacea generally, though Borradaile holds that the maximum number is nine, which would include the doubtful "precoxa" of the trilobite.

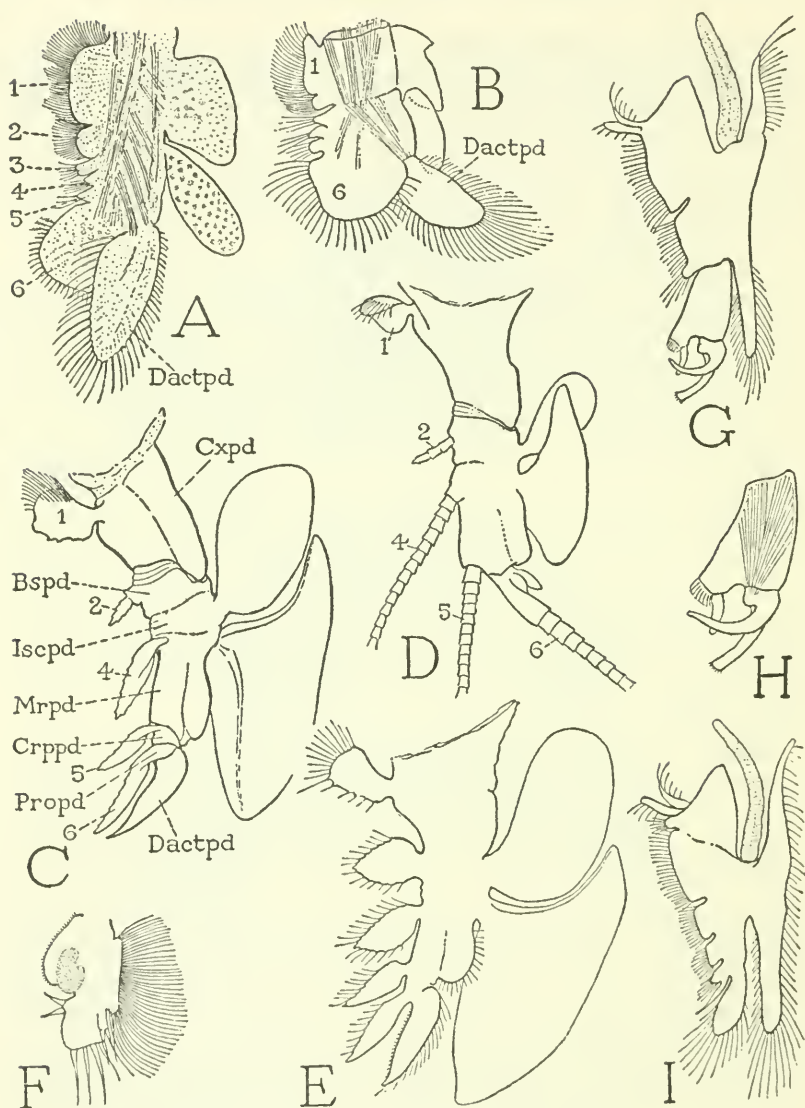


FIG. 27.—Examples of branchiopod appendages.

A, *Branchipus stagnalis*, Anostraca, thoracic limb (from Claus, 1873). B, *Branchipus serratus*, male, eighth thoracic limb. C, *Apus longicaudata*, Notostraca, second maxilliped. D, same, first maxilliped. E, same, thoracic limb from middle of body. F, *Daphnia magna*, Cladocera, third thoracic appendage (from Hansen, 1925). G, *Estheria clarkii*, Conchostraca, second thoracic limb. H, same, terminal segment. I, same, left limb from middle of body.

Bspd, basipodite; Crppd, carpopodite; Cxpd, coxopodite; Dactpd, dactylopedite; Iscpd, ischiopodite; Mrpd, meropodite; Propd, propodite; 1-6, endites.

There are two chief objections to this phyllopod theory of the origin of jointed crustacean limbs. First, it gives no explanation of the origin of the similarly jointed legs of other arthropods, except by the wholly unsupported assumption that they likewise were developed from phyllopodial limbs. Second, the ontogenetic development of the crustacean appendages themselves gives no evidence of a phyllopodial origin, and suggests, on the contrary, that the phyllopodium has been evolved from an ambulatory leg.

The study by Heath (1924) of the postembryonic development of the branchiopod *Branchinecta occidentalis* shows very clearly that the limbs arise as simple, lateroventral lobes of the body segments (fig. 3 B). Instead of taking on a phyllopodial shape, the rudiments grow out first in a slender leglike form (C, D). On the inner margins of the appendages at this stage there are indentations suggestive of an incipient segmentation, and at the apex is a terminal lobe. Only at a later stage (E) do the appendages become broad overlapping flaps. Finally in the adult (F) the appendages have taken on the form of typical unsegmented phyllopodia with three large flat exites, six endites, and a free, independently muscled terminal lobe. Clearly, these appendages in their ontogenetic development undergo a metamorphosis from an ambulatory leg into a phyllopodium. Though Heath himself did not have this phase of the subject in mind, his pictures speak for themselves.

Conversely, as seen in Heegaard's (1953) account of the postembryonic stages of the decapod crustacean *Penaeus setiferus*, the rudiments of the pereopods develop directly into legs without undergoing any stage suggestive of a phyllopodial origin. The pereopods appear during the second protozoal stage as simple lobes on their respective body segments (fig. 28 A). In the third protozoa they take on a biramous structure (B), in which the protopodite, at first undivided, bears a short unsegmented endopodite and a longer exopodite. In the second mysis stage (C) the limbs attain a fully segmented structure by the division of the protopodite into two segments and the endopodite into five, with a terminal chela on each of the first three. The exopodites are now large seta-bearing branches of the basipodites used for swimming. In the postmysis (D) the pereopods have become essentially uniramous by the reduction of the exopodites to small lobes, and the swimming function has been taken over by the pleopods. This condition is retained in the adult. If the pereopods of *Penaeus* had a phyllopodial origin in their phylogeny, there is nothing to suggest it in their ontogeny. The mouth-part appendages proceed along their own lines of development to serve the special functions they have assumed

as organs of feeding. The pleopods (E) and the uropods (F), on the other hand, appear to remain in an early stage of development represented by the simple, unsegmented biramous stage of the pereopods (B).

The swimming appendages of the anostracan branchiopods so regularly have six mesal lobes (figs. 3 F, 27 A, B) and a movable terminal

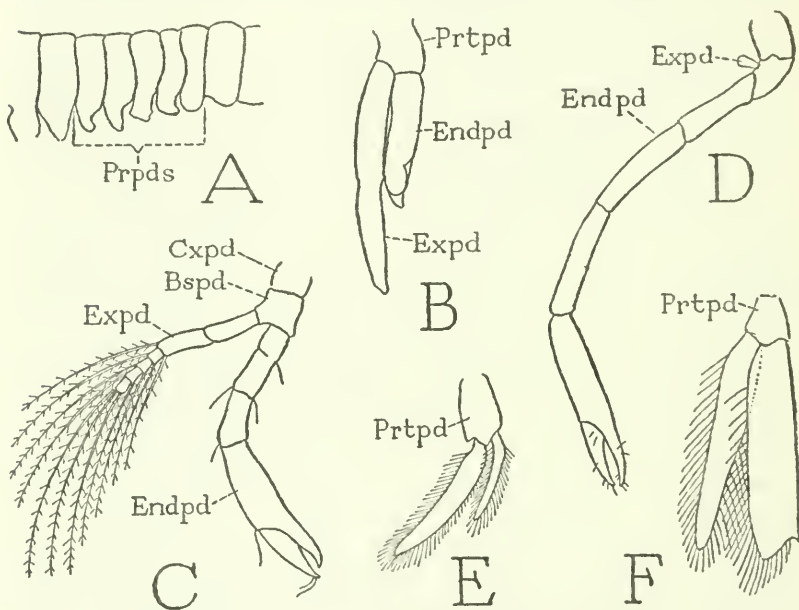


FIG. 28.—Development of the pereopods and pleopods of *Penaeus setiferus* (L.) (from Heegaard, 1953).

A, rudiments of pereopods on thoracic segments of second protozoaea. B, pereopod of third protozoaea. C, pereopod of second mysis instar. D, third pereopod of postmysis. E, second pleopod of young adult. F, uropod of postmysis.

Bspds, basipodite; *Cxpds*, coxopodite; *Endpd*, endopodite; *Expd*, exopodite; *Prpds*, pereopod rudiments; *Prtpd*, protopodite.

lobe as to suggest that the six endites represent the first six segments of a leg (coxopodite to propodite) and the independently muscled apical lobe the dactylopodite. Yet, the sixth endite is commonly interpreted as the endopodite and the apical lobe as the exopodite. In the notostracan *Apus*, however, the second maxilliped (fig. 27 C) is a seven-segmented leg ending with a clawlike dactylopodite (*Dactpd*) and having an endite on each of the other segments except the ischiopodite. The first maxilliped of *Apus* (D) is somewhat simpli-

fied, but the swimming appendages (E) clearly retain the structure of the second maxilliped. In other branchiopods the appendages may be variously reduced (F, G, H, I) obscuring the basic leg structure.

The segmentation of the arthropod legs is surprisingly constant; variations result from the elimination of segments, seldom from addition, though the propodite (tarsus) is generally rendered flexible by subdivision. If all the podomeres in the legs of the trilobite (fig. 25 A) and *Marella* (B) are true muscled segments, the ancient arthropods had eight limb segments, including a small apical dactylopodite, or pretarsus, and thus possessed all the segments that are present in any of the legs of modern arthropods. Among the latter, eight segments are present in the Pycnogonida and in some of the legs of the arachnid Solpugidae (D), but in most of the arachnids the leg has only seven segments by the elimination of the third segment from the base. The segment beyond the knee bend (D, *Pat*), which is the fifth segment in the trilobite leg (A), is called the patella, though it might appear to correspond with the carpopodite (tibia) in the leg of a centipede (E) or a decapod (F). Yet there are three segments beyond it in the spider leg, and only two in the other arthropods. In the latter, therefore, either two original segments in the distal part of the leg are united, or one has been eliminated. The legs of the chilopods and the decapods (E, F) have seven segments; the insect leg has only six segments because of the apparent union of the ischiopodite (second trochanter, or prefemur) with the meropodite (femur).

Though the primitive arthropods (fig. 1 C) undoubtedly were aquatic, they were walking animals provided with jointed limbs, and probably lived on plants in shallow water near the shore. Their habits may have been similar to those of the modern *Anaspides* (D). The typical jointed ambulatory leg has been retained in all modern arthropods, except in those crustaceans in which it has been modified for swimming, but even the phyllopodium preserves evidence of the seven-segmented structure of a walking leg. It would appear that the primitive arthropods had more legs than they needed for walking, and because of this fact their descendants have been able to reconstruct many of them into the great variety of appendicular organs possessed by modern forms. The arthropods owe what they are, as well as their name, to their jointed appendages.

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THE VENTRAL INTERSEGMENTAL
THORACIC MUSCLES OF
COCKROACHES

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THE VENTRAL INTERSEGMENTAL THORACIC MUSCLES OF COCKROACHES

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The cockroaches, which have persisted in much their present outward form since the Carboniferous, are admittedly rather primitive in many structural respects. Although one dares not take for granted that their musculature also retains a primitive configuration, there is a good *a priori* chance that this is the case; and comparisons with other primitive types, such as *Grylloblatta* (Walker, 1938, 1943), the larvae of *Dytiscus* (Speyer, 1922) or *Cybister*, and larval or adult Megaloptera, to my mind leave no doubt that the muscular pattern of blattids displays many primitive characteristics.

In this paper attention will be called to certain of these features, as they are seen in the ventral intersegmental musculature of the thorax. This system of muscles, though far from homogeneous morphologically, provides a convenient segment of the total thoracic musculature for analysis. It may also be regarded as itself a relatively primitive component of pterygote anatomy, for study of the more recently evolved, highly specialized flying insects shows the ventral intersegmental muscles of the thorax gripped in an evolutionary trend that has already led to the drastic reduction of these muscles and that may ultimately result in their total disappearance. In contrast, the cockroaches and other less advanced forms still exhibit a wealth of muscles in this category, and thus afford some conception of this portion of the ancestral basis from which the more adept flying insects of today have developed.

Descriptions of the thoracic musculature have already been published for three blattid species: *Blatta orientalis* L., by Miall and Denny (1886); *Periplaneta australasiae* (L.), by Maki (1938); and *P. americana* (L.), by Carbonell (1947). Miall and Denny purposely gave only a general account; and comparisons of the reports by Maki and Carbonell discloses more numerous and in some instances more

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striking differences among the ventral intersegmental muscles than one would ordinarily expect from members of the same order, not to say genus. Since a precise knowledge of the distribution of the ventral muscles is essential if one is to draw from them conclusions concerning thoracic evolution, a reinvestigation of these species was made, in the course of which it became apparent that familiarity with a wider variety of blattids would be helpful. Eventually 19 species were examined. The discussion below attempts to extract from this material information that illuminates certain important facets of the evolution of the thorax in winged insects.

METHOD AND MATERIAL

Specimens from culture were etherized, pinned venter-down in a wax dish, and covered with water. Under binoculars, the dorsal integument was carefully cut away from thorax and abdomen, after which the ventral system of muscles was gradually exposed by removing structures that interfered with the view. A few details were checked from other angles. Liberal staining with 1 percent methylene blue from time to time in the course of dissection proved helpful, and brief hardening in 70 percent alcohol was occasionally resorted to. The magnification used was 12.5 to 50 times. At various stages of dissection drawings were made to scale on squared paper with the aid of a micrometer eyepiece.

P. americana (L.), *Blaberus craniifer* (Burm.), *Blatta orientalis* L., *Blattella germanica* (L.), and *Supella supellectilium* (Serv.) were available in our laboratory. Cultures of the following species were supplied through the generosity of F. H. Babers, J. H. Fales, W. L. Nutting, L. M. Roth, P. R. Ruck, C. N. Smith, and E. R. Willis: *P. australasiae* (L.), *P. brunnea* Burm., *P. fuliginosa* (Serv.), *Blaberus giganteus* (L.), *Blattella vaga* (Heb.), *Cryptocercus punctulatus* Scud., *Diploptera dytiscoides* (Serv.), *Eurycotis floridana* (Walk.), *Leucophaea maderae* (Fabr.), *Nauphoeta cinerea* (Oliv.), *Neostylopyga rhombifolia* (Stoll), *Parcoblatta pennsylvanica* (DeGeer), and *Pycnoscelus surinamensis* (L.). A single preserved specimen of *Macropanesthia rhinocerus* Sauss. also was dissected. The 19 species investigated were chosen mainly on the basis of availability and are but a small fraction of the more than 3,500 species of cockroaches that (*vide* Rehn, 1951) have been described.

Nymphs and adults of both sexes were examined for most species, although few differences attributable to stage or sex were found among the muscles to which the present investigation was confined. For comparison, data were obtained from the literature or from the

writer's dissections for representatives of a number of other orders. All observations cited in this paper without a statement as to source are from my own work.

Each morphologically distinct muscle was given a designation formed by hyphenating the accepted abbreviations for the skeletal parts between which the muscle is stretched. Under this system, if an attachment is segmental, the segment is identified by an arabic or roman postsubscript for the thorax or abdomen, respectively, while the designations of intersegmental structures are preceded by the appropriate arabic numeral, beginning with *o* for the cervical intersegment. *Exception:* the customary abbreviations *icv*, *zcv* . . . for the cervical sclerites, and *iax*, *zax* . . . for the axillary sclerites of the wing, the latter with segmental subscripts, are retained. Cruciate muscles, with origin and insertion on opposite sides of the longitudinal body axis, are distinguished by adding *X* to the usual designation. The skeletal abbreviations used are for the most part those given currency by Snodgrass (1929, and numerous other publications).

Examples: *zsps-eps₃*, a muscle stretched between the second (post-mesothoracic) spina(stermite) and the metepisternum; *fu₃-sIIA*, the longitudinal ventral muscle from the metafurca to the second abdominal sternum; *eps₂-cx₁X*, a cruciate muscle of the procoxa, with origin on the contralateral mesepisternum.

A glossary of abbreviations is given at the end of the text.

OBSERVATIONS AND INTERPRETATION

The ventral intersegmental muscular system of the blattid thorax includes elements with primary attachments on the spinae (*sps*) or on the intersegmental laterosternites (*ils*), as well as furcal (*fu*) muscles that run between successive segments. This report is divided accordingly into three main sections.

I. THE SPINAE

Cockroaches have two authentic spinae (*1sps*, *2sps*), and in addition possess in the third thoracic intersegment a common junction of serial homologs of the more anterior spinasternal muscles that lacks the median connection with the integument but obviously represents a postmetathoracic spina. This junction ("*3sps*") is attached by fibrous ligaments (figs. 4, 6, 7, 9, 10, 18:27) to the bases of the metathoracic furcal arms (*fu₃*), between which it floats above the nerve cord. Comparative evidence leaves little doubt that these non-contractile ligaments, which now usually appear as *fu₃-fu₃*, have been

derived from former muscles, *3sps-fu₃*. A true third spina, which occurs in some Apterygota (Maki, 1938), is known among pterygote insects only in *Grylloblatta* (Walker, 1938, 1943), but an arrangement much like that of blattids has been reported for larval *Dytiscus* (Speyer, 1922) and has also been seen in larval *Cybister*, in *Zootermopsis* (fig. 6), and in larval and adult *Corydalus*. Other vestiges of the third spina and its musculature have been found but not recognized as such by several students in a number of other insects. Altogether, the facts constitute strong evidence that a third spina was present in the ancestral Pterygota, and probably in early hexapods generally.

More thoroughly documented, since much of the testimony is still available in a variety of living forms, is a general tendency toward loss of the remaining spinae and their associated musculature during the post-Carboniferous evolution of the pterygote thorax. Certain cockroaches, however, have gone contrary to this trend, and have experienced a prodigious extension of the first spina and, to a lesser extent, the second, in the direction of the body axis. Compare, for example, figure 1 with figure 2, or 17 with 18. This spinal elongation is related, in part, to hypertrophy of the transverse spinal musculature (*1sps-cps₂*, *2sps-cps₃*); and it is probably no coincidence that several species that manifest this development have also exceptionally large transverse muscles of the first abdominal intersegment, *sIIA-sIIA* (figs. 1, 8, 11, 12: 34). My judgment that these characteristics are secondary rests partly upon the fact that they are peculiar to some blattids, being unparalleled in others and absent, so far as I know, in any other group of insects; and partly upon the presence in the musculature of these same cockroaches of other trends away from a primitive condition, such as a tendency toward loss of certain spinacoxal muscles. (See c, this section, below.)

Table 1 provides a composite list of the spinasternal muscles of blattids, as these are now known, and is so arranged as to indicate the probable serial homologies. Most species possess a very large fraction of the total complement. The relatively few exceptions are summarized in footnotes to the table, and some of them are discussed briefly in the text. Included in the spinasternal musculature are (a) transverse spinal muscles; (b) spinal muscles of the preceding or succeeding furca; (c) spinal muscles of the preceding or succeeding coxa; (d) muscles stretched between successive spinae; and (e) spinabdominal muscles. Each of these groups is discussed under the corresponding subheading below.

a. *Transverse spinal muscles*.—The transverse muscles of cock-

TABLE I.—*Spinasternal muscles of cockroaches*

In this composite list, muscles that appear on the same horizontal line are considered serially homologous. Question marks indicate uncertain homologies. Symbols such as *M*₄₀, *C*₁₀₃ refer to the numbers given the corresponding muscles in *P. australasiae* by Maki (1938) and in *P. americana* by Carbonell (1947). Each of the 19 species investigated here has all muscles shown in the table, except as stated in the notes below or in the text. For muscles without spinasternal attachments, see table 2.

Footnote number	First spina	Second spina	"Third spina"
1,a	<i>1sps-1ils</i>	<i>2sps-2ils</i>	---
1,b	<i>1sps-eps₂</i>	<i>2sps-eps₂</i>	---
	<i>M</i> ₄₀ ; <i>C</i> ₁₀₃	<i>M</i> ₇₄ ; <i>C</i> ₁₄₉	
2	<i>1sps-fu₁</i>	—	"3sps"- <i>fu₂</i>
	<i>M</i> ₈ ; <i>C</i> ₉₉	<i>M</i> ₄₁	<i>M</i> ₁₀₅ (<i>partim</i>)
3	—	<i>2sps-fu₁</i>	---
		<i>C</i> ₁₀₁	
4	<i>1sps-fu₂</i>	<i>2sps-fu₂</i>	? "3sps"- <i>s</i> _{IIA}
	<i>C</i> ₁₀₄	<i>M</i> ₇₃ ; <i>C</i> ₁₅₁	<i>M</i> ₁₀₄ ; <i>C</i> ₁₉₁ ?
5	—	<i>2sps-s</i> _{IIA}	---
		<i>C</i> ₁₈₉	
6	<i>1sps-cx₁</i>	<i>2sps-cx₂</i>	? <i>fu₂-cx₂</i> , <i>post. rot.</i> (<i>partim</i>)
	<i>M</i> ₂₄ , 25; <i>C</i> ₉₈	<i>M</i> ₅₆ ; <i>C</i> ₁₃₄	<i>M</i> ₈₈ , 89; <i>C</i> ₁₇₁
7	<i>1sps-cx₂</i>	<i>2sps-cx₂</i>	---
	<i>C</i> ₁₀₅	<i>C</i> ₁₇₃	
8	<i>1sps-2sps</i>	<i>2sps-3sps</i>	? "3sps"- <i>ventr. diaphr.</i>
	<i>M</i> ₃₉ ; <i>C</i> ₁₀₆	<i>M</i> ₇₂ ; <i>C</i> ₁₅₂	<i>M</i> ₁₀₅ (<i>partim</i>)

¹ *Cryptocercus* has both 1,a and 1,b; other species 1,b only. The abdominal transverse muscle, *s*_{IIA-s}_{IIA} (*M*₁₁₂, is a serial homolog.

² Muscle *2sps-fu₂* is lacking; Maki's record (*M*₄₁) is probably an error of transcription. (See text.)

³ No comment.

⁴ Carbonell (1947, p. 20) describes muscle *191* in *P. americana* as follows: "Oblique ventral muscle. . . . From the base of the sternal arm to the anterior edge of the first [sic!] abdominal sternum."

⁵ Abdominal insertion wholly or partly on *s*_{IIIA} in *Eurycotis*, *Macropanesthia*, *Neostylopyga*, and *Periplaneta brunnea*. (See text.)

⁶ Several species have two definitive muscles, *1sps-cx₁*, one of which is probably equivalent to the *eps₂-fu₁* of other species. (See figures and text.) In listing two furcal posterior rotators of the third coxa, Maki (1938) suggests that one of them may be serially homologous with the spinal posterior rotators of the other legs. (See text for discussion.)

⁷ *Blaberus*, *Diploptera*, *Cryptocercus*, *Leucophaea*, *Macropanesthia*, *Nauphocta*, and *Pycnoscelus* lack *1sps-cx₂*; the last five genera also lack *2sps-cx₂*.

⁸ The fibers from "3sps" to the ventral diaphragm were not found in several species, but were possibly destroyed during dissection in some of these.

roaches are regularly present in the first two thoracic intersegments but absent in the third, where their failure to appear is no doubt related to the near obliteration of the ventral region of the first abdominal segment, reduction of which is a very general and probably very early feature of pterygote reorganization. However, the transverse muscles are represented in the abdomen by the muscular attachments of the ventral diaphragm on the anterior lateral angles of the second abdominal sternum. A striking development of these abdominal fibers is seen in the series *Pycnoscelus*, *Diploptera*, *Nauphoeta*, *Leucophaea*, in which last they attain the status of a powerful transverse muscle, $s_{IIA}-s_{IIA}$ (figs. 1, 8, 11, 12: 34). The function of such a muscle is unknown. Curiously, *Blaberus*, *Cryptocercus*, and *Macropanesthia* (figs. 5, 10, 17), which share other peculiarities of the four genera just mentioned, do not show any tendency toward hypertrophy of the transverse muscle of the ventral diaphragm, and in this respect are more like the other species included in this study. The lateral suspensions of the ventral diaphragm are not evident in the abdominal intersegments posterior to the first; and in general the ventral diaphragm of cockroaches is much less extensive than that of some other insects, e.g., phasmids and the acridid Orthoptera.

Some authors have listed as transverse muscles structures such as the ligament fu_3-fu_3 , whose affinities are, however, with the spinafurcal muscles.

b. Spinafurcal muscles.—Cockroaches all have the muscle $1sps-fu_1$ and " $3sps$ "- fu_3 , the latter represented, as a result of loss of the third spina, by fibrous ligaments that often appear as a single transverse band, fu_3-fu_3 . A corresponding $2sps-fu_2$ does not occur in any blattid I have examined, and I believe Maki's record of this muscle (1938, fig. 6, No. 41) in *P. australasiae* must rest on an error of transcription, since all cockroaches have another, larger muscle, $2sps-fu_1$, that is omitted from his figure and description.

Miall and Denny's (1886) statement that the muscle $2sps-fu_1$ is inserted on the base of the first leg in *B. orientalis* is misleading, for the connections in *B. orientalis* (fig. 2: 16) are identical with those of other cockroaches; but the description reflects Miall and Denny's awareness of a structural difference between the prothoracic sternal arm and those of other segments, a distinction that seems to have escaped comment by most others who have investigated the musculature of cockroaches. (See section 3, below.)

The muscles $1sps-fu_2$ and $2sps-fu_3$ are also universally present in blattids as is their possible serial homolog, " $3sps$ "- s_{IIA} , which is here

discussed under the spinabdominal muscles. (See e, this section, below).

c. *Spinacoxal muscles*.—The first and second spinae both carry posterior rotators (or remoters) of the preceding coxa (*1sps-cx₁*, *2sps-cx₂*) in all blattids examined. A corresponding muscle of the third spina is absent as such, but may be represented, as already suggested by Maki (1938), in the muscle *fu₃-cx₃ post. rot.*, which frequently shows signs of a dual composition. In some specimens, a few of the fibers of *fu₃-cx₃ post. rot.* appear to be continuous with those of the ligament *fu₃-fu₃*. Only in larval *Dytiscus* (Speyer, 1922), in *Grylloblatta* (Walker, 1938, 1943), in *Zootermopsis* (fig. 6: 29), and in the larvae of *Cybister* and *Corydalus* has a distinct muscle, *3sps-cx₃*, been found; and in these species the muscle *fu₃-cx₃ post. rot.*, which is also present, seems to be a single band.

Spinal *promotors* of the mesocoxa and metacoxa (*1sps-cx₂*, *2sps-cx₃*) also occur frequently in cockroaches, as they do in other primitive forms. However, the mesocoxal promotor is absent in *Blaberus*, *Diploptera*, *Leucophaea*, *Macropanesthia*, *Nauphoeta*, and *Pycnoscelus*; and the last four of these genera also lack the metathoracic homolog. Both spinal promotors are likewise missing in *Cryptocercus*, which shares to some extent the tendency of these genera toward hypertrophy of the transverse muscles of the first spina although it differs markedly from them in certain other respects. In some other cockroaches, e.g., in *Blattella*, the spinal promotors, though present, are weak. Thus, the trend toward obliteration of these muscles, which has gone far among higher orders of insects, is evident even among the Blattariae.

d. *Spinaspinal muscles*.—The muscles *1sps-2sps* and *2sps-“3sps”* were found in all the species studied here, although they are at times weakly developed and easily overlooked; this is particularly true of *2sps-“3sps.”* The first of these muscles is present also in most Orthoptera (*sensu stricto*) and Mantodea, but not in other orders with the possible exception of Isoptera, where it was recorded by Fuller (1924, fig. 9, muscle *n*) for *Termes latericius* Hav. Since this muscle does not occur in other termites studied by Maki (1938) and the writer, it may be that Fuller misjudged the posterior attachment of his muscle *n*, which perhaps represents *1sps-fu₂*, a muscle missing from Fuller's account but present in all Isoptera studied by others.

The muscle *2sps-“3sps”* has so far been recorded only from blattids, where its general occurrence may be taken as one more indication of primitive structure. What is probably a vestige of this muscle

has been found in the immature mantid, *Tenodera sinensis* Sauss. (fig. 7: 23).

The spinaspinal muscles are the only portion of the longitudinal ventral musculature that has obviously retained its primary relationships in blattids. Both attachments are still unmistakably intersegmental. Like the other somatic muscles, the spinaspinal muscles are paired bilaterally; but the right and left bands of *1sps-2sps* are often so closely appressed in the midline that they seem like a single element, and they have been so described by some authors. The posterior insertions of *2sps*-"*3sps*" are usually well separated on the ligament *fu₂-fu₃* (c.g., fig. 9: 23), and in some instances may even seem to be on *fu₃* at the site of attachment of the ligament. Care must be taken, therefore, not to confuse them with the usually better developed spinafurcal muscles, *2sps-fu₃*, from which they are morphologically distinct.

The ligament *fu₂-fu₃* also serves, in several cockroaches, as a base of attachment for paired muscular strands that course posteriorly to join the meshwork of contractile fibers and membrane that constitutes the ventral diaphragm (figs. 2-5, 8, 11, 18: 30). These strands, "*3sps*"-ventr. diaphr., may be serial homologs of the muscles *1sps-2sps*, *2sps*-"*3sps*." I did not succeed in finding these delicate strands in all species, but could not be sure, in the cases where they seemed absent, that I had not destroyed them.

In pterygote insects, there is no homolog of the spinaspinal muscles anterior to *1sps*; but Maki (1938) has recorded muscles that are probably homologous in the prothorax of some Apterygota.

e. *Spinabdominal muscles*.—The spinabdominal muscles of cockroaches include only *2sps-s_{IIA}*, "*3sps*"-*s_{IIA}* and "*3sps*"-ventr. diaphr. The last two have already been mentioned in this section, b and d, above. They arise on the ligament *fu₂-fu₃*, and not on the base of *fu₃* as some have stated. The muscle *2sps-s_{IIA}* is characteristic of blattids, and is present in all of them I have seen, though it is weak in *Leucophaea*. Elsewhere, it has been recorded only from *Grylloblatta* (Walker, 1938, No. 111b). It is interesting as an example of a muscle more than one segment in length, a type that is of infrequent occurrence in pterygote insects. In *Macropanesthia*, *Periplaneta*, *Eurycotis*, and *Neostylopyga* the abdominal insertion of some or all the fibers is actually on *s_{IIIA}*. Apparently this modification may occur readily because *2sps-s_{IIA}* is ordinarily inserted along the antecosta of *s_{IIA}* dorsal to the usual longitudinal bands, *s_{IIA}-s_{IIIA}*, with which *2sps-s_{IIA}* is more or less continuous. Dissolution of the integumental attachment at *s_{IIA}* adds one segment of muscle

to the length of $2sps-s_{IIA}$; and this step, to judge by various instances observed, leads to an intervening stage in which the now floating muscle is still divided by a transverse septum at the original level of attachment on s_{IIA} (figs. 3, 17: 21). Subsequently, all signs of the septum are lost. Reduction of the ventral region of the first abdominal segment has doubtless contributed to developments of this nature, which are not confined to cockroaches or to the particular muscle in question (cf. fig. 11: 32).

2. THE INTERSEGMENTAL LATEROSTERNITES

Intersegmental laterosternite (*ils*) is a term here introduced for sites of muscle attachment that lie at the lateral extremities of the ventral intersegmental folds. Such sites are believed to have been characteristic features of the anatomy of early arthropods in all intersegments. In existing forms, extensive modification of the original relationships is the rule, as will be seen below; nevertheless, recognition of the presence and nature of these sites is helpful in understanding the manner in which the ventral musculature and associated structures have evolved.

Primitively, the musculature of the *ils* included (1) the transverse muscles, which, with or without interruption by a median spina, stretched between the two *ils* of the same intersegment; (2) the outermost bands of the ventral longitudinal body musculature; (3) certain dorsoventral muscles; and probably (4) other muscles of various types, some of which will be noted below. However, the original muscular relationships of the *ils* are still not fully understood; and this fact, together with their varied fate in different lines of descent and in different parts of the body, presents the comparative morphologist with many perplexing problems. Hence, it is not surprising that structures equivalent to the *ils* as here defined have been overlooked by some workers and variously named in different situations by others. Several have referred to them as "intersegmental pleurites," a term which is unsatisfactory both because of the obvious sternal nature of the structures in question and because use of the name "pleurite" in reference to intersegmental elements is self-contradictory. Crampton (1926) avoided these objections by employing the term "furcilla." Unfortunately, this usage of "furcilla" seems likely to cause confusion, because the name had been applied in various other senses by earlier workers and because it suggests a nonexistent affinity with the segmental sternal apophyses, or "furcae" (*fu*). For these reasons, we have substituted the more accurately descriptive designation "*ils*."

The principal primary muscular relationships of the *ils* are tolerably well preserved in the typical abdominal intersegment, granted that a secondary extension of sclerotization has here merged the intersegment indistinguishably with the following segmental sternal plate, of which the former intersegment now forms the antecosta (Snodgrass, 1929). The *ils* are here represented in the anterolateral angles of the definitive abdominal sterna, which in many insects display the muscular relationships outlined above (Ford, 1923; Maki, 1938).

In the intersegments that follow each of the three thoracic segments, the situation is rarely so transparent. One gains the impression that, even in the most primitive forms that have come to hand, the musculature of the *ils* has already been subject to extensive shifting and reduction, while in more recent insects only a few scattered remnants suggest the original role of the *ils* as attachment sites for part of the longitudinal body muscles. Moreover, where the transverse muscles have been preserved, their lateral attachments now usually appear to be on segmental parts. In addition, we find a few muscles that originate on the thoracic *ils* or on their present equivalents, whose insertions are segmental and which have no counterparts in the legless abdomen.

Equally difficult to analyze, because of the extremely varied skeletal and muscular relationships that exist in different groups, is the situation in the cervical intersegment. Here one must be content for the present with the assurance that the former *Oils* are usually somehow represented, most often as part of one or more of the definitive cervical sclerites.

These problems are well illustrated in the cockroaches, in which the musculature of the *ils*, though rich in comparison with that of more recently differentiated orders, can only be considered vestigial in relation to the inferred ancestral condition.

Ventral muscles of cockroaches that appear to belong to the *ils* complex include (a) transverse muscles; (b) cruciate coxal and furcal muscles; (c) certain other furcal muscles; and (d) spinasternal muscles of the abdominal *ils*. (See tables 1 and 2.)

a. *Transverse muscles*.—The transverse muscles of the thorax ordinarily have a median attachment on the spina, and have therefore been discussed under section 1,a, above. The nature of their lateral attachments remains to be considered. As already noted, abdominal relationships support the view that the lateral attachments of the transverse muscles are morphologically intersegmental, i.e., on the *ils*. Comparative evidence from other arthropods and the scanty em-

bryological data on insects (Heymons, 1895; Roonwal, 1937) justify this inference. In the postembryonic cockroach, however, the definitive connection in the thorax is usually with the anterior margin of the succeeding episternum, and the muscles are therefore to be designated as *1sps-eps₂*, *2sps-eps₃*, even though Maki (1938, p. 58) describes the attachment as "on the small sclerite before the [mes]episternum" in *P. australasiae*. If this were all the evidence available, one would conclude that in blattids the *1ils* and *2ils* had fused with

TABLE 2.—*Ventral intersegmental muscles of cockroaches: muscles without spinasternal attachments*

Symbols such as M6, C55 refer to the numbers given the corresponding muscles in *P. australasiae* by Maki (1938) and in *P. americana* by Carbonell (1947). For muscles with spinasternal attachments, see table 1.

Footnote number	Muscle type			
1...	Cruciate muscles	<i>1cv-cx₁X</i>	<i>eps₂-cx₁X</i> C97	<i>eps₂-fu₁X</i> C102
2...	Postcoxal ligaments	<i>1ils-fu₁</i>	<i>2ils-fu₂</i>	<i>3ils-fu₃</i>
3...	Furcal muscles	<i>fu₁-tent.</i> M6; C55 <i>fu₁-fu₂</i> (2 bands) M38; C100 <i>fu₂-fu₃</i> (2 bands) M71; C148 <i>fu-s_{IIA}</i> (usually 3 bands) M103; C192, 193	<i>fu₁-2cv</i> M7; C84	

¹ The 3 cruciate muscles are not serially homologous. For discussion of shifts in origin of *eps₂-cx₁X* and *eps₂-fu₁X*, see text sections 2,a and 2,b. The three muscles or their equivalents are present in all species examined.

² The three postcoxal ligaments are serially homologous. For variations in their occurrence, see text section 2,c.

³ The furcal muscles are probably all serially homologous, at least in a broad sense. For variations in the abdominal insertion of *fu-s_{IIA}*, see text section 3. Carbonell (1947) records the abdominal attachment of muscles number 192 as on *s_{IA}* in *P. americana*. All the furcal muscles listed are present in all species investigated.

eps₂ and *eps₃*, respectively. The arrangement of the cruciate muscles of the profurca and procoxa in *P. americana* and in *Cryptocercus* (see below) is also consistent with this interpretation.

However, the full story is not that simple, for *Cryptocercus* possesses not only muscles *1sps-eps₂*, *2sps-eps₃* that are clearly homologous with those of other blattids, but has in addition fibrous ligaments (figs. 10, 13: 4, 17) that run from the spinae to small sclerites in the intersegmental membrane well in advance of the episternal margin. These transverse ligaments have evidently been derived from former muscles, and their lateral attachment sites not only occupy the

position of true *ils* but also carry the dorsoventral muscles typical of these structures.

Furthermore, careful dissection of most cockroaches discloses a second series of straplike ligaments, also of muscular derivation, that run from the postcoxal membranes (i.e., from the intersegments) to the furcal arms of the respective preceding segments. These ligaments, here designated *ils-fu₁*, etc., are inserted on the furcal arms near the seat of the furcophragmatal muscle (see figs. 2, 10: 13, 24, 31).

It appears, then, that in the thoracic intersegments of cockroaches the former *ils* may now be represented by as many as three seemingly distinct sites: (1) the following episternum; (2) the original *ils*; and (3) the origin of the postcoxal ligament. How this separation came about is by no means obvious.

As already stated, the often straplike but still fibrous transverse ligaments *Isps-ils*, etc., are evidently derived from former muscles, and are even now represented in whole or in part by muscles in some species. However, again in the light of relationships found in other primitive groups (e.g., *Dytiscus* larva (Speyer, 1922), *Corydalus* larva, etc.), these transverse muscles seem to have served also (after loss of their contractile nature ?) as suspensory ligaments for a portion of the longitudinal ventral intersegmental musculature. Vestiges of this or an analogous arrangement are still present in the first thoracic intersegment of some cockroaches.

In *Cryptocercus*, which in this respect is the most primitive blattid I have seen, both the ligament *Isps-ils* and the muscle *Isps-eps₂* are present and are, laterally, quite distinct (fig. 13: 4, 5). However, the mesal portion of *Isps-ils*, incidentally still composed of contractile tissue, is so confluent with the adjacent fibers of *Isps-eps₂* that a separation of the two muscles in this region is hardly possible. Thus, the anterior portion of the muscle *Isps-eps₂* could be described as "ligament-*eps₂*." Similarly, it is difficult to specify the origin of the cruciate profurcal muscle *eps₂fu₁X* (8), for part of its fibers arise on *eps₂* while the more ventral ones, not visible in figure 13, originate on the ligament *Isps-ils*, from which they run with the others to the insertion on the contralateral furcal apodeme *fu₁*.

Variations of these relationships are exemplified in a number of other genera, viz, *Periplaneta*, *Neostylopyga*, *Eurycotis*, *Blatta*, and *Blattella*. In none of these is the peripheral attachment of the ligament *Isps-ils* preserved; but the central portion of the ligament is present and extends anterolaterally from the spina as a noncontractile septum on which fibers from *eps₂* are attached and from which origi-

nate muscles ("*eps₂*"-fu₁X, "*eps₂*"-cx₁X) that insert on the contralateral profurca and procoxa. These conditions in *P. brunnea* are illustrated in figure 14. Here it will be noted that the origin of the cruciate furcal muscle (8) is more central than that of the cruciate coxal muscle (9). In *P. australasiae* (fig. 15: 8) the more dorsal bands of the furcal muscle originate so near the midline that they appear to arise from the spina; and they are so recorded in Maki's (1938) description.

The contrasting arrangement of the corresponding muscles in *P. americana* is apparent in figure 16. In this species, there is no visible remnant of the ligament *Isps-ils*, and the cruciate muscles (8, 9) originate far laterally, on the anterior margin of *eps₂*, as they were described by Carbonell (1947). Hence the structure of *P. australasiae* and *P. americana* is superficially quite distinct. Access to intervening forms, such as *P. brunnea*, etc., shows, however, that in *P. australasiae* and *P. americana* we are merely confronted with rather extreme variations in the arrangement of morphologically identical elements.

Cryptocercus is unique among the cockroaches studied in that the most dorsal fibers of the transverse muscle of the first intersegment, *Isps-eps₂*, continue across the body without attachment on the spina (fig. 13: 5). This development is almost certainly secondary, for the more ventral fibers of this muscle have the usual spinal connection.

The several variants we have seen in the cruciate muscles are such that all of them could have been derived, by gradual transition, from any one chosen as a starting point. There is also at present no bar to the alternative assumption that any or all of them might suddenly have arisen *de novo* from each other or from an unknown basic pattern as a result of gene mutation or recombination. Therefore, a decision as to which of the existing configurations portrays the most primitive condition is not warranted on the basis of the evidence so far presented. Although *Cryptocercus* shows some very primitive features in the first thoracic intersegment, it is even here less primitive in other respects than certain other cockroaches, and should not be regarded as the prototype for the arrangement of the cruciate muscles unless independent confirmation can be produced. Other data that bear on this question are cited in this section, b, below.

At the present time, it also does not seem possible to decide whether muscles such as *Isps-ils* and *Isps-eps₂* are fundamentally distinct, or whether the episternal branch is no more than a hypertrophied offshoot from an originally single transverse band. Both elements are present simultaneously in a few other insects, not all of which are

closely related to the cockroaches. An example is shown in figure 6: 4, 5. There is some indication also, in various other primitive groups, that there existed muscles of the type *ils-eps₂*; if so, these too may have contributed to the arrangements now seen in blattids, for they could conceivably account for the lateral portions of the cruciate muscles that run in some species from *eps₂* to the transverse ligament *isps-ils* or to the septum that has replaced it.

b. Cruciate coxal muscles.—Mention of the cruciate coxal muscle, *eps₂-cx₁X* (9), has been made in the preceding section. This muscle is inserted together with the spinal posterior rotator *isps-cx₁* (7), from which it is morphologically distinct. However, species such as *P. australasiae*, in which the origin of "*eps₂*"-*cx₁X* is far mesad, could properly be described as having two definitive spinacoxal posterior rotators, as was done by Maki (1938, fig. 6, Nos. 24, 25). In most instances these two muscles may still be distinguished by the fact that the true spinal muscle originates along the side of the spina ventral to the other spinal musculature, whereas the muscle equivalent to *eps₂-cx₁X* has a more dorsal origin, anterior to the transverse muscle *isps-eps₂*. Yet the distinction is not always clear; and in some blattids one or the other of these two muscles may even have been lost.

Serial homologs of the muscle *eps₂-cx₁X* do not occur in cockroaches so far as is known, but homologs with origins on the *ils* are found in all three thoracic segments of larval *Dytiscus* (Speyer, 1922) and in larval *Cybister*. In larval *Corydalus*, which lacks such muscles in the first intersegment, cruciate posterior rotators of the second and third coxae originate on the corresponding furcal arms. This shift in origin is easily understood from the fact that the furcal arms are here fused with the succeeding *ils*, evidently, as judged by conditions still found in some other Megaloptera such as *Sialis* spp., in consequence of sclerotization along the line of the postcoxal ligaments *zils-fu₂*, *zils-fu₃*. One infers from the position of the cruciate coxal muscles in these primitive forms that the attachments of the cruciate muscles of cockroaches on *ils* or *eps₂* are more likely the primary ones than any of the other variants observed in blattids. If so, *Cryptocercus* and, for some strange reason, *P. americana* but not its congeners have more nearly preserved the original condition.

Cruciate promoters of the first coxa have been described from a number of orders, and are apparently present in a much reduced state in all cockroaches, although on account of their delicacy they have escaped the notice of myologists. In the adult insect, which is the stage usually chosen for dissection, they are extremely slender and

transparent. They are more easily seen, though not immediately recognizable as muscles, in the nymph, where they were first discovered by Scharrer (1948) as the bearers of the prothoracic glands. The glandular tissue, which encases the tenuous contractile filament and thus renders it more visible (fig. 7: 3), degenerates soon after metamorphosis, but the muscular core persists throughout life. The origin is near the anterior end of the first cervical sclerite, *1cv*, which for this and other reasons is to be regarded as incorporating the cervical *ils*; and the insertion is on the proximal margin of the contralateral coxa vera, just laterad of the coxotrochantinal articulation. Corresponding cruciate promotor of the second and third coxae have not been identified in any pterygote insect, but there is a possibility that they are represented in the usual spinal promotor *1sps-cx₂*, *2sps-cx₃*.

c. *Lateral furcal intersegmental muscles*.—In cockroaches furcal muscles whose origins are on the *ils* or on their present equivalents include only the cruciate muscles *eps₂-fu₁X* of the first intersegment; and the three postcoxal ligaments *1ils-fu₁*, etc. The cruciate muscle has been discussed in the preceding sections.

The postcoxal ligaments are often frail and transparent, and therefore easily overlooked in dissection; and they dissolve rapidly in alkali. These characteristics no doubt explain why the ligaments have not received more attention from morphologists, for they are quite frequently present in primitive insects. (See fig. 6: *13*, *24*, *31*, and fig. 7: *24*, as well as the figures of cockroaches.)

By a process that has many analogies in the evolution of the pterygote thorax, the postcoxal ligaments have often been replaced, in phylogeny, by apodemal growths, a course of development that culminates in a firm skeletal union between the furcal arm and the succeeding *ils*. Such unions constitute, or at least contribute to, the postcoxal bridges, whose interpretation has interested several previous students of insect morphology.

Cockroaches, however, show little or no indication of the trend toward formation of a postcoxal bridge by sclerotization along the line of this former muscle. Only in *Blaberus*, of the blattids I have seen, is the distal end of the ligament *2ils-fu₂* converted into a stiff, well-sclerotized apodeme; whereas the usual course of evolution of a postcoxal bridge in other Pterygota seems, contrariwise, to have been via sclerotization from the furcal attachment outward.

In fact, the general impression left by the blattids is that their tendency is toward obliteration of these ligaments, and this tendency is increasingly manifest as one passes from the prothorax to the metathorax. All the cockroaches studied possess a fairly strong and

short *ils-fu₁*; and a longer and more slender *zils-fu₂* was found in all but *Pycnoscelus*. The presence of *zils-fu₃* was definitely ascertained only in the genera *Periplaneta* (4 species), *Eurycotis*, *Blatta*, and *Cryptocercus*. Failure to find a structure of this delicate nature is, of course, no proof of its absence; but the observations cited nevertheless do indicate quite well the tendency for these ligaments to weaken in the more posterior segments. The genera where their presence in the metathorax is most doubtful (*Leucophaea*, *Nauphoeta*, etc.) are notably those judged to have a more specialized muscular pattern on the basis of other criteria; and several of these are large insects, where such a structure, if present, should be relatively easy to find.

The origins of the postcoxal ligaments of cockroaches, though clearly intersegmental, are at sites anterior and dorsal to the small sclerites identified as the true *ils* by their reception in *Cryptocercus* of the transverse ligaments and of the usual dorsoventral muscles. In some other insects, the two sites are closer together or even indistinguishable, and I can offer no explanation for their separation in blattids.

d. *Spinasternal muscles of the abdominal ils*.—Only two such muscles have been found in cockroaches, namely *zsps-s_{IIA}* and "*zsps*"-*s_{IIA}*. The usual abdominal attachments for both are near the anterolateral angle of the second sternum, somewhat anterior and ventral to the suspension of the ventral diaphragm. As explained above, this region of the definitive sternite is believed equivalent morphologically to the thoracic *ils*.

Identification of this attachment site with the *ils* renders dubious the homology, indicated as possible in table 1, of "*zsps*"-*s_{IIA}* with the spinafurcal muscles *1sps-fu₂*, *zsps-fu₃*; for it is very unlikely that the *ils* have contributed to the furcal structures of cockroaches. (See this section, c, above.)

The muscle from the second spina *zsps-s_{IIA}* clearly has no serial homolog in blattids. It is ordinarily inserted on *s_{IIA}* somewhat mesad and ventrad of "*zsps*"-*s_{IIA}*, and is thus two full segments in length. The variant attached on *s_{IIIA}* has been discussed in section 1, c.

3. THE FURCAE

The consensus of morphologists has been that the furcae (*fu*) of higher insects have been produced, in phylogeny, by the approximation in the ventral midline of paired segmental sternal apophyses (Weber, 1928; Snodgrass, 1929). The resulting Y-shaped structure

consists of the infolded furcabis and the laterally extended furcal arms. In cockroaches, as in other primitive forms, right and left apophyses remain separate. For this reason, purists avoid applying the term "furca" to them, but for convenience we shall continue to refer to them as the furcae or furcal arms, with which they are homologous. Despite the seemingly incontestable segmental nature of these apophyses, they nevertheless carry a large fraction of the surviving longitudinal ventral intersegmental musculature in all pterygote insects. This situation poses a contradiction, long recognized and accepted by students of thoracic structure, that has never been satisfactorily resolved (cf. Snodgrass, 1929).

Weber (1928) surmised that the present furcal intersegmental muscles had been derived from spinasternal muscles. He proposed that, as the furcal arms were gradually elevated in phylogeny, they intercepted the spinasternal muscles, which thereupon acquired furcal attachments and lost their primary connections with the spinae. This hypothesis, which regards the furcal muscles as replacements for the spinasternal muscles, is clearly untenable in the face of the presence of the usual complement of furcal intersegmental muscles in all those primitive forms, such as larval *Dytiscus* (Speyer, 1922) or *Cybister*, larval *Corydalus*, and the cockroaches, which still retain an extensive spinasternal musculature, including (in the blattids) both spinaspinal muscles *1sps-2sps*, *2sps-3sps*. Conceivably, the rising furcal arms could have intercepted some of the more lateral bands of the primary ventral longitudinal intersegmental muscles, for instance those attached on or below the transverse ligaments, *1sps-tils*, etc.; but even this modification of Weber's hypothesis is unconvincing in the absence of any known situation in insects where interception of a muscle by a skeletal element has led to the development of an attachment between the two. Moreover, the data of Carpentier, Barlet, and others (see Barlet, 1954, for references) show that the essential features of the furcal complex exist in the Apterygota, which also possess an extensive array of muscles homologous with the spinasternal muscles of higher forms. Any notion that the furcal longitudinal muscles have arisen in the Pterygota through transfer of muscles from some other category must therefore be abandoned. How then can they be accounted for?

An answer may be approached, we believe, through realization that the principal endoskeletal structures of insects and other arthropods have all developed as the result of sclerotization along the course of former muscles, and that the present sternal arms are of this nature. Although the genesis of certain endoskeletal structures lies so far in

the past that it will probably be impossible forever to document the details of the process in these instances, there are many other cases where the course of evolution can be deduced with reasonable certainty from comparisons of existing forms. The complex endosternal structures of the Apterygota furnish a number of examples, for, as described by the Belgian authors cited above, many endosternal elements that are ligamentous in one species or group are still represented by functional muscles or by apparently degenerate muscles in others. In the opinion of the present writer, yet other parts of the endosternum that are invariably ligamentous in the apterygote species so far studied are homologous with muscles, such as the transverse muscles, that persist as contractile elements in some primitive Pterygota and as ligaments in others. Another clearcut set of examples of the replacement of muscles by endoskeletal structures is found in the later history of the sternal arms themselves, for instance in the development of the furcopleural fusion, which has occurred independently in numerous lines of descent. Here the process can be followed in some detail through several series of intermediate stages provided by existing forms.

As a generalization we offer the hypothesis that all such endoskeletal developments owe their inception to other structural or functional changes that have limited freedom of movement at the insertions of certain muscles. These muscles, deprived of their original effectiveness as contractile organs, are doomed to disappear unless they happen to retain some value in the role of static supports or braces. Furthermore, the organism evidently finds it more economical to construct the braces it requires from other than contractile tissue, which cannot resist compression and which can maintain tension only through a continuous expenditure of energy, so that replacement of bracing muscles or tensors by noncontractile ligaments or by stiffer sclerotized apodemes is the usual evolutionary pattern. In our view, structures originating in this manner constitute the primary endoskeletal rudiments. Once established, these may be variously molded in later evolution in accordance with the mechanical requirements they are called upon to fill; and in the course of such modification their original derivation from muscles may be almost wholly obscured.

Returning to the narrower problem of the nature of the sternal arms and their longitudinal musculature, we may point out that the arms are represented in the Apterygota by ligamentous straps that connect the thoracic endosterna, which are mainly intersegmental in character, with the respective preceding segmental sternal regions (references in Barlet, 1954). In these insects the endosterna provide the

attachment sites for almost all the ventral musculature, including, of course, the usual longitudinal intersegmental muscles. We have already indicated our belief that the entire endosternal complex, which is ligamentous in consistency, is of muscular derivation; and we suggest here that the sternal ligaments are merely another example of transformed muscles. We may then regard the endosternum schematically as a point of junction of various intersegmental muscles, among which are the usual longitudinal bands and a muscle to the preceding segmental sternum.

The configuration thus summarized is, however, exactly what is seen in the musculature associated with the sternal arms of pterygote insects. True, the number of elements that impinge upon this focus is less than in the Apterygota; but those elements that do occur in the Pterygota all have their counterparts in muscles that are attached on the apterygote endosternum in proximity to the attachments of the sternal ligaments, or in similarly directed portions of the endosternum itself. Only the fact that the sternal arm of Pterygota is usually a heavily sclerotized ingrowth of the ventral body wall gives the superficial impression of a fundamental difference between the two subclasses.

In cockroaches, even this distinction breaks down; for in the prothorax of blattids the paired furcal pits do not give rise at once to sclerotized apodemes, as they do in the mesothorax and metathorax, or in the prothorax of most Pterygota. Instead, there extends inward from the pit a flexible, fibrous ligament that connects with the apex of a sclerotic bar whose other end articulates firmly with the pleural apodeme. Upon this bar, at or near its junction with the sternal ligament, are inserted the usual muscles of the furcal complex.

On the basis of these facts and the considerations outlined above, we suggest that the sternal arms of pterygote insects represent muscles that formerly ran from the segmental sternal region posteriorly to a common junction of various other intersegmental muscles, including the forerunners of the present longitudinal furcal muscles. In the course of evolution, the sternal muscles were replaced first by non-contractile ligaments, a condition still manifest in the Apterygota and in the prothorax of blattids, and finally by sclerotized apodemes, the form in which they now appear in the pterothorax of cockroaches and in all three thoracic segments of most winged insects. These changes in the sternojunctional muscle have not altered the morphological relationships of the other muscles attached at the junction, which may still be regarded as an intersegmental locus in the morphological sense.

There is thus no problem of explaining a shift of their attachments to a segmental site, for no shift has occurred.

Apart from the structure of the profurca, with its connotations for the evolution of the furcal structures of pterygote insects in general, there is little that is remarkable about the sternal apophyses and their musculature in cockroaches that has not already been touched on in preceding sections. The ventral furcal intersegmental muscles found in the Blattariae may be classified as (a) spinafurcal muscles; (b) furcal muscles from the *ils*; and (c) furcofurcal muscles, including muscles with furcal origins and insertions in the head, neck, or abdomen. If the suggestion offered above is correct, that the definitive furcal apophysis is partly of intersegmental nature, a number of other muscles with furcal attachments, such as those of the appendage, may also be primarily intersegmental. However, further work is needed on the details of such relationships, and it seems best to leave them for future consideration.

Except for muscles with spinasternal attachments (table 1), the ventral furcal intersegmental muscles of cockroaches are listed in table 2.

Furcal muscles from the spinae and *ils* have been discussed above, particularly under sections 1,b, 2,a, and 2,c. Like these muscles, the furcofurcal muscles of blattids can be homologized in considerable detail with those of comparable location in other insects. Readily distinguished in most cockroaches are a usually slender mesal band and a more massive lateral band of both fu_1 - fu_2 and fu_2 - fu_3 . Components probably homologous with each of these bands can also be identified in many blattids in the muscle fu_3 - s_{IIA} , which often includes an additional more ventral group of fibers. These subdivisions, ordinarily lumped together in descriptions, seem to possess a fair degree of constancy in a number of insect orders, and may be of significance in future more detailed comparative studies.

The fact that the furcabdominal muscles are inserted on the second (never on the first) abdominal sternum, is what would be expected if the furcal attachment is really intersegmental, as has been argued above. Morphologically, these muscles still run from the third thoracic intersegment to the first abdominal intersegment, and have neither lost nor shifted their original attachment sites. However, just as the muscle $2sps$ - s_{IIA} has become $2sps$ - s_{IIIA} in some species (section 1,e), so is a portion of fu_3 - s_{IIA} found, at times, as fu_3 - s_{IIIA} , as a result of an analogous development (figs. 1, 5, 8, 11, 12, 17: 32).

The profurca bears two anteriorly directed longitudinal ventral intersegmental muscles. The stronger, consisting of two or more bands and serially homologous with the muscles fu_1-fu_2 , fu_2-fu_3 , passes into the head to insert on the tentorium. This muscle, fu_1-tent (figs. 1-18: 1), is commonly considered to be more than one segment in length (Snodgrass, 1935, p. 159). The weaker, usually a thin, flat strap of somewhat degenerate appearance, has a more ventral origin on fu_1 (figs. 4, 5, 9: 2) and is inserted on the mesal lobe of the ipselateral second cervical sclerite. Possibly this site should be referred to the *Oils*, which are certainly included in the first cervical sclerites, *Icv*, of which the *2cv* may be merely subdivisions (Crampton, 1926); but this question cannot be settled until the constitution and muscular connections of the various cervical structures of insects are better understood.

GENERAL DISCUSSION

Reinvestigation of the ventral intersegmental muscles of the three cockroaches previously studied by others has shown each of the earlier accounts deficient in some respects. The defects are mostly errors of omission. Thus, none of the earlier investigators noted the muscle *Icv-cx₁X* or the three postcoxal ligaments *iils-fu₁*, etc. That they did not is understandable, for these are hardly muscles in a functional sense, even though the cervicocoxal "muscle" does have a contractile core a few microns in diameter. Carbonell's (1947) exclusion of the ligament $fu_3-fu_3 (=3sps-fu_3)$ and of the bands "*3sps*"-ventr. *diaphr.* from his description is likely to have been on similar grounds; for in most other details his depiction of *P. americana* is accurate and complete. However, unless Maki's (1938) specimens of *P. australasiae* differed radically from those of this species available to the writer, one must reject Maki's assertions that the muscles *1sps-fu₁*, *1sps-cx₂*, *2sps-fu₁*, *2sps-cx₃*, and *2sps-s_{IIA}* are absent, and that a muscle, *2ps-fu₂*, unknown in any other cockroach, is present. Miall and Denny (1886) stated explicitly that they had not given a complete account of the muscles of *B. orientalis*, so that there is no cause for surprise in the fact that this species has numerous muscles unmentioned in their description.

When these few corrections have been made, it is seen that all species of cockroaches thus far studied have nearly identical complements of ventral intersegmental muscles. The spinasternal promoters of the coxae, *1sps-cx₂* and *2sps-cx₃*, are absent from some species and show signs of weakness in others. The metathoracic post-

coxal ligament *3ils-fu₃* is either lacking or very frail in several genera. *Cryptocercus* alone of the species investigated possesses muscles as yet found in no other blattid; these are the semiligamentous transverse bands *1sps-1ils* and *2sps-2ils*, parts of which seem to have survived as septa in some other cockroaches. With these minor exceptions, the differences among the several species are merely variations in relative size and proportions of the various muscles, or occasionally in their position. Such differences, some of them quite conspicuous, obviously indicate shifts in functional emphasis, although in most instances the details of their interpretation from this viewpoint are obscure.

In contrast with most modern insects, the cockroaches enjoy a relatively rich ventral intersegmental musculature. Some authorities would be inclined, perhaps, to regard this as a consequence of secondary reduction of sclerotization in the ventral regions of the blattid thorax; but acceptance of this view would make it very hard to account for the presence of homologous muscles in a number of other groups in which the thorax is extensively sclerotized. There is no muscle recorded in this paper for which either a direct or a serial homolog has not been found in at least one other order of pterygote insects, and most of them are known from several. Coupled with the fact that those other orders that display a similar degree of complexity in the ventral intersegmental musculature are the ones considered highly primitive in various other respects, the evidence seems more consistently interpreted in the conclusion that the cockroaches also are primitive in this feature, and that the primitive state of the ventral intersegmental muscles was a complex one. As already indicated in the introduction, the various structural patterns preserved for our scrutiny among the more recently evolved orders of insects, which constitute a progressive series of specializations toward greater efficiency in flight, show that improvement in the flight mechanism has been accompanied regularly by reduction in the ventral intersegmental thoracic musculature. These facts also favor the view that the possession of numerous discrete muscles in this category is a primitive characteristic. The results of a more comprehensive inquiry into these problems will be reported elsewhere.

SUMMARY

1. A comparative study was made of the ventral intersegmental musculature of the thorax in 19 species of cockroaches. The observations produced a few corrections, mainly additions, to earlier de-

scriptions of 3 of these species. In general, there are very minor differences among the species in respect to the presence or absence of individual muscles in the category studied, although there are numerous differences, some conspicuous, in the relative size and proportions of the various muscles.

2. The present ventral intersegmental thoracic muscles had their primary attachments on the spinae, on the intersegmental laterosternites, or on the forerunners of the furcal apophyses. Cockroaches still have two typical spinae and definite vestiges of a third. They possess an extensive spinasternal musculature. Remnants of the musculature of the intersegmental laterosternites are present, but some of these muscles now have segmental attachments, and others are represented by noncontractile ligaments. The longitudinal furcal muscles are equivalent to those of other pterygote insects.

3. Attention is called to the postcoxal ligaments that run between the furcal apophysis and the immediately following intersegmental laterosternite in each of the thoracic intersegments, and to the significance of these former muscles in the development of the postcoxal bridges of higher insects.

4. Evidence and arguments are presented for the hypothesis that the furcal apophyses represent former muscles that have been replaced in phylogeny by sclerotized apodemes. It is suggested that one attachment of these muscles was on the segmental sternum, the other at a common intersegmental junction of several other muscles, among them elements of the longitudinal ventral group. Loss of movement at the sternal insertion led first to transformation of the sternojunctional muscle into a fibrous ligament and eventually to the sclerotization of the ligament. Analogous events have occurred frequently in the evolution of the pterygote thorax. The blattid prothorax exemplifies a stage in the evolution of the typical furcal apophysis when the postulated sternal muscle was still in a ligamentous condition. The subsequent sclerotization of this ligament, which has occurred in the other thoracic segments of cockroaches and in all three segments of most Pterygota, in no way alters the morphological relationships of the other muscles inserted upon its central end; morphologically, then, the present attachments of the longitudinal ventral muscles on the furcal arms are still intersegmental, and it is therefore unnecessary to invent mechanisms whereby they might have been shifted from an intersegmental to a segmental site of attachment.

5. The ventral intersegmental thoracic musculature of cockroaches is rich in number of elements, compared to that of more recently

evolved groups. However, direct or serial homologs of all the elements occur in one or more other orders of winged insects. The most extensive complements of these muscles are found in those forms, such as larval dytiscids, Grylloblattodea, and Megaloptera, that are regarded as primitive on the basis of other criteria. It is concluded, therefore, that the blattids also are primitive in respect to the ventral intersegmental muscles; and that possession of a rich ventral intersegmental musculature was characteristic of the early Pterygota.

ACKNOWLEDGMENT

The writer is grateful to Dr. R. E. Snodgrass for helpful discussion of several questions considered in this paper.

GLOSSARY OF ABBREVIATIONS

<i>cv</i>	cervical sclerite
<i>cx</i>	coxa
<i>eps</i>	episternum
<i>fu</i>	furca, furcal arm, segmental sternal apophysis
<i>ils</i>	intersegmental laterosternite
<i>ph</i>	phragma, or the primary dorsal intersegmental fold from which the phragma is derived
<i>post. rot.</i>	posterior rotator, a functional designation used to distinguish certain leg muscles
<i>s</i>	segmental sternum
<i>sept.</i>	septum
<i>sps</i>	spinasternite or spina
<i>t</i>	segmental tergum
<i>tent.</i>	tentorium
<i>ventr. diaphr.</i>	ventral diaphragm
<i>X</i>	cruciate, used of a muscle whose origin and insertion are on opposite sides of the midline

For the way in which these abbreviations are compounded into designations of muscles, see section on Method and Material in text.

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EXPLANATION OF FIGURES

All muscles figured are numbered uniformly according to the list below. Instances in which the definitive attachments differ from those given in the list have been discussed fully in the text.

The arrangement of ventral muscles in certain species is such that not all of them can be shown in a single drawing. However, all cockroaches studied have all muscles given in the list, whether the muscles appear in the figures or not, except as noted under tables 1 and 2 or in the text. The termite *Zootermopsis* (fig. 6) and the mantid *Tenodera* (fig. 7) have only the ventral intersegmental muscles shown in the drawings.

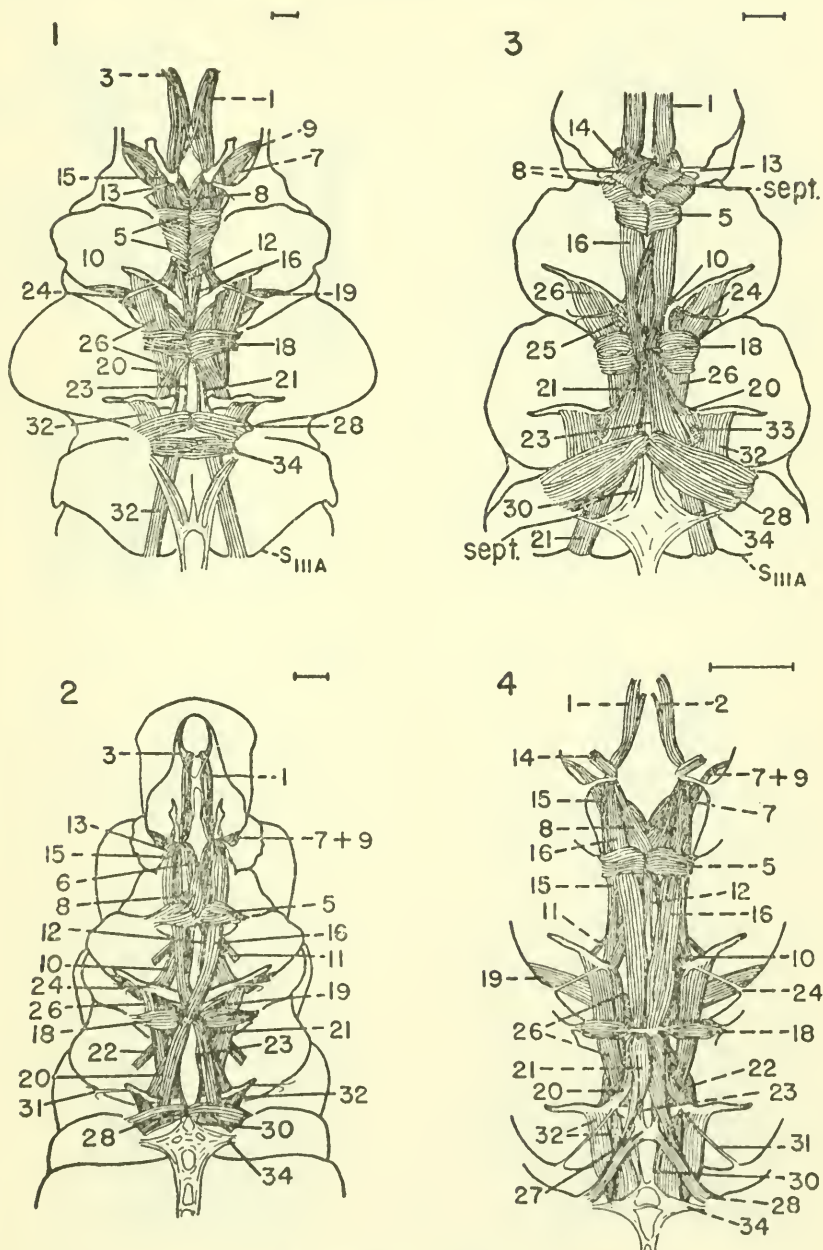
In a few instances different levels of dissection have been shown in different parts of the same figure; this does not imply an absence of the usual bilateral symmetry. To assist in orientation, some figures contain a few muscles that do not belong to the ventral intersegmental category.

The scale indication represents 1 mm.

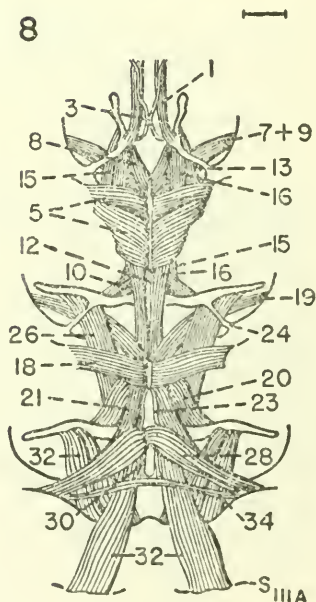
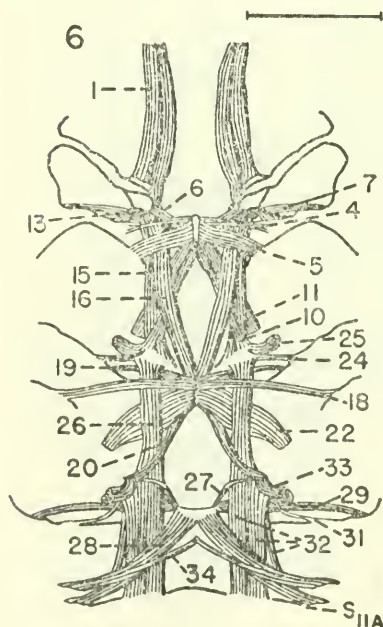
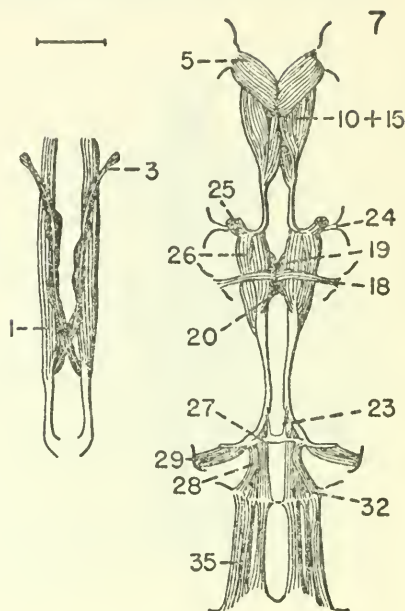
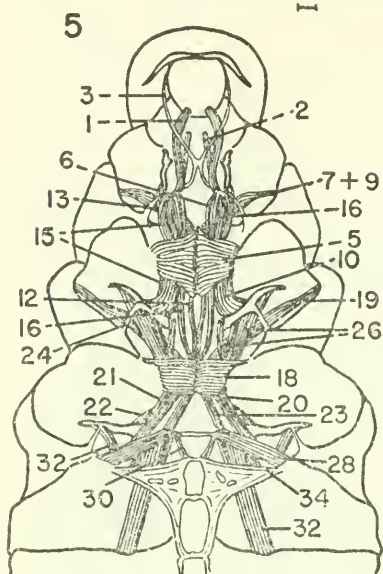
NUMBERING OF MUSCLES IN FIGURES 1-18

Number	Muscle	Number	Muscle	Number	Muscle
1	<i>fu₁-tent.</i>	13	<i>ils-fu₁</i>	25	<i>fu₂-2ph</i>
2	<i>fu₁-2cv</i>	14	<i>fu₁-1ph</i>	26	<i>fu₂-fu₃</i>
3	<i>1cv-cx₁X</i>	15	<i>fu₁-fu₃</i>	27	<i>"3sps"-fu₃</i>
4	<i>1sps-ils</i>	16	<i>2sps-fu₁</i>	28	<i>"3sps"-s_{IIA}</i>
5	<i>1sps-cps₂</i>	17	<i>2sps-2ils</i>	29	<i>fu₃-cx₃ post. rot.*</i>
6	<i>1sps-fu₁</i>	18	<i>2sps-cps₃</i>	30	<i>"3sps"-ventr. diaphr.</i>
7	<i>1sps-cx₁</i>	19	<i>2sps-cx₂</i>	31	<i>3ils-fu₃</i>
8	<i>cps₂-fu₁X*</i>	20	<i>2sps-fu₃</i>	32	<i>fu₃-s_{IIA}*</i>
9	<i>cps₂-cx₁X*</i>	21	<i>2sps-s_{IIA}*</i>	33	<i>fu₃-3ph (or -t_{IA})</i>
10	<i>1sps-fu₂</i>	22	<i>2sps-cx₃</i>	34	<i>s_{IIA}-s_{IIA}</i>
11	<i>1sps-cx₂</i>	23	<i>2sps-3sps</i>	35	<i>s_{IIA}-s_{IIIA}</i>
12	<i>1sps-2sps</i>	24	<i>2ils-fu₃</i>		

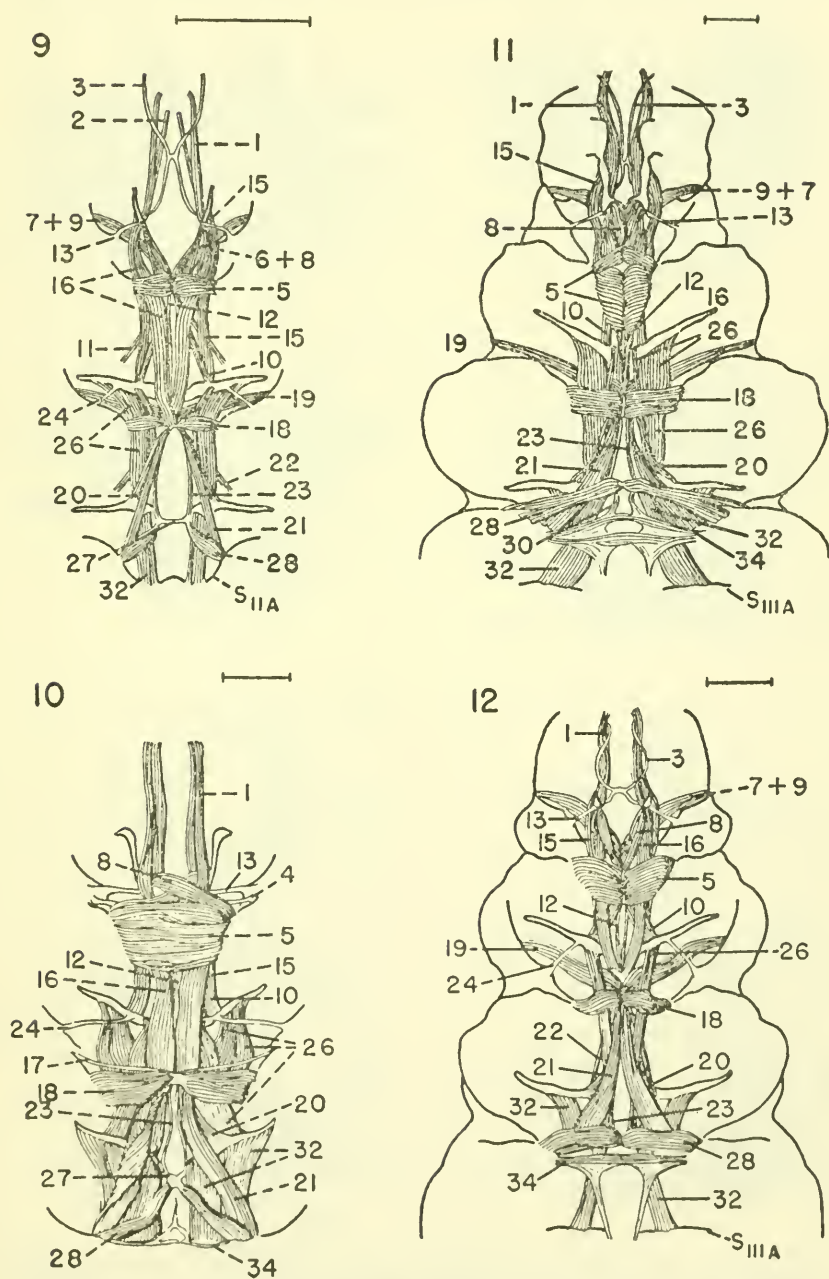
* Variants from these attachments are discussed in the text.



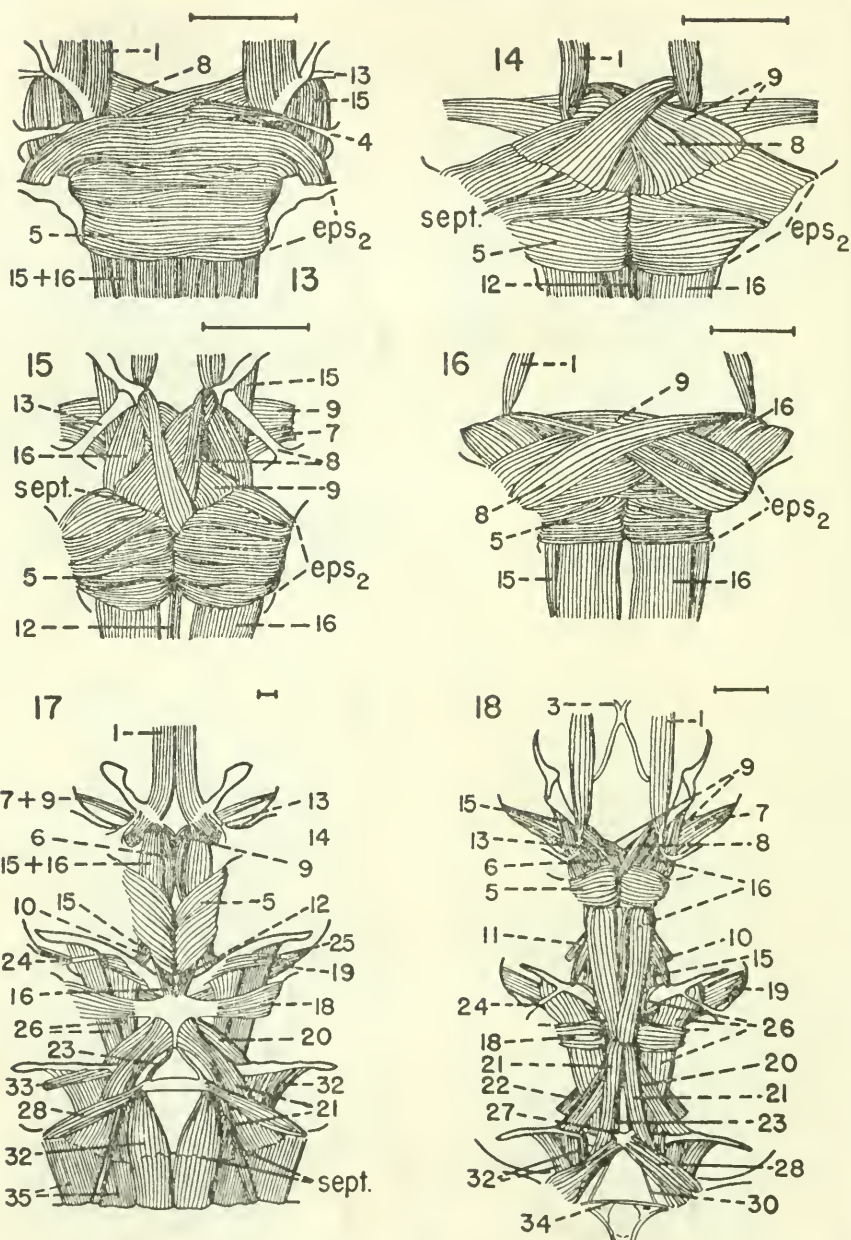
FIGS. 1-4.—1, *Leucophaea maderae* (Fabr.), male. 2, *Blatta orientalis* L., male nymph. 3, *Neostylopyga rhombifolia* (Stoll), male. 4, *Blattella vaga* (Heb.), female.



FIGS. 5-8.—*Blaberus craniifer* (Burm.), nymph. 6, *Zootermopsis angusticollis* (Hagen), worker (Isoptera). 7, *Tenodera sincensis* Sauss., nymph (Mantodea). The prothorax is shown on the left, the mesothorax and metathorax on the right. The portion of the prothorax posterior to the sternal arms, which does not carry any ventral intersegmental muscles, has been omitted. Glandular tissue that invests the muscles *lev-cr₁X* (3) is shown in solid black. 8, *Nauphoeta cinerea* (Oliv.), nymph.



FIGS. 9-12.—9, *Supella supellectilium* (Serv.), female. 10, *Cryptocercus punctulatus* Scud., female. 11, *Pycnoscelus surinamensis* (L.), female. 12, *Diploptera dytiscoides* (Serv.), nymph.



FIGS. 13-18.—13, *Cryptocercus punctulatus* Scud., female, detail of first thoracic intersegment. 14, *Periplaneta brunnea* Burm., nymph, detail of first thoracic intersegment. 15, *Periplaneta australasiae* (L.), nymph, detail of first thoracic intersegment. 16, *Periplaneta americana* (L.), nymph, detail of first thoracic intersegment. 17, *Macropanesthia rhinocerus* Sauss., female. 18, *Parcoblatta pennsylvanica* (DeGeer), nymph.

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